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

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Running header: Multivariate ecosystem functioning

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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 – IG: https://isabellegounand.wordpress.com, CL: https://chelseajeanlittle.com, EH: https://metecolab.org, FA: https://www.altermattlab.ch)
**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 which 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.
Multivariate ecosystem functioning

Keywords

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

Ecosystems provide multiple services, such as food, carbon storage, or 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 which 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 on 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 Fig. 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 with 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, nutrients). Stocks, fluxes, and rates – the three dimensions of our ecosystem functioning space – relate 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 of adopting 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., BEF 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 & McKee (2002)). A comparative synthesis of ecosystem functioning would reveal potential covarations 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 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 et al., 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 to characterize 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 Fig. 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 covariation 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 metabolic theory of ecology.

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, i.e., mass-specific GPP = GPP/autotroph biomass, and decomposition rate as described by the k constant) from the literature (Fig. 1a), for eight major ecosystem types, both terrestrial (forest, grassland and shrubland–thereafter called “grassland” for simplicity–, agroecosystem, and desert) and aquatic (stream, lake, ocean pelagic, 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 Fig. 1b for the combinations considered and Table S1.1 of Appendix S1 in Supporting Information 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 informs about producers’ biological efficiency and physiological constraints, while GPP also includes information on their abundance. We aimed at covering a wide range of ecosystem x climate x variable combinations, and retrieved at least ten independent values for each of these
combinations (see Appendix S1 for extended methods and a decision tree on study selection for data collection, and Appendix S2 in Supporting Information 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 (Fig. 2), extracted from 604 published studies. The list of data sources is provided in Appendix 1.

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$^{-1}$, and year$^{-1}$, respectively (noted as “g g$^{-1}$ year$^{-1}$” 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 Table S1.2 for factors). Flux and rate data provided on timescales 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 centimetres depth. Complete details on these unit conversions are provided in extended methods (see 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: (1) 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; (2) 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; (3) 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 x C combinations due to different numbers of data points. Because the residuals were not homogenously distributed, we repeated the model design using more conservative non-parametric 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 non-parametric tests give the same results on effect significance, so we report ANOVAs results here to visualize the variance partitioning, and non-parametric tests are reported in the supporting information (see full statistical results in Appendix S3 in Supporting Information, Tables S3.1 to 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 x Climatic zone combination (E x C), and tested the correlation between variables with 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 (Appendix S2.4, Figs S2.10 and S2.11, Table S3.13). Finally, we synthetize the average trends in ecosystem functioning by displaying the median values of each E x 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 point per E x C x 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 covered on multiple climatic zones (agroecosystem and desert were excluded) using Pearson’s two-sided correlation tests (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 originates 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 3.3.3, 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 Appendix S1 for more details. Final artwork was realized with Illustrator CC 22.0.1.

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 Fig. 3) according to both parametric and non-parametric tests (see Tables S3.1-S3.5). Main and interactive effects (C, E versus C:E) for each ecosystem variable are all highly significant (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 (Table S3.2). When considering individual ecosystem variables, the 2-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%) (Fig. 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 ecosystem respiration (ER) is relatively homogenous across ecosystems (see Fig. 4c, Tables S3.6 and S3.7). Lastly, 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 Fig. 4a and Table S3.1), indicating that the direction of climatic effects varies across ecosystem types.
3.2 | Stocks, fluxes, and rates’ variation 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 (Figs. 5 and 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 (Fig. 5a), and those displaying high GPP also show high ER (Fig. 5b). While such 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 Fig. S2.10, and discussion in Appendix S2.4), 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, and pelagic marine systems (Figs. 5a, 5b), while rates are higher in streams and pelagic marine ecosystems than in the rest of ecosystem types (see Fig. 5c; see significantly different groups in Table S3.4). Stocks generally correlate positively with fluxes, such as biomass with GPP, but negatively with rates, such as biomass with uptake rate (Fig. 5 panels d and e, and Fig. S4.1), the later relation being also strongly conserved within ecosystems (Fig. S2.10). Thus, in systems sustaining more standing biomass, more biomass is produced in total but at a lower rate. The negative stock-rate relationships, however, does not hold for detritus and decomposition rates (Fig. 5f; but see the relatively opposed directions of these variables in a PCA on median ecosystems in Fig. S4.2).

Overall, positioning median ecosystems in the three-dimensional space of stocks, fluxes and rates results in a gradient of functioning types (Fig. 6): forest ecosystems have the largest stocks and fluxes but low rates. Grasslands also have relatively slow biological
Multivariate ecosystem functioning

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 Fig. 6).

3.3 | Climatic modulation

A climatic imprint is most visible on fluxes and decomposition rates (Figs. 4a, 4b, Tables
S3.1 and S3.2). In comparison, stocks vary less, and less consistently, with climate (Figs
4b, 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 (Fig. S4.3, Table
S3.8). By contrast, GPP, ER and rates systematically decrease with latitude (Figs 7,
S4.4), although the relationship is not significant in all ecosystem types: for instance,
GPP does not correlate with latitude in streams (Fig. 7a). This absence of a climatic effect
was also apparent when using discrete climatic zones (see Fig. 4c and Table S3.6).
Moreover, different responses of GPP and ER to latitude within ecosystem types might
result in opposite response of Net Ecosystem Production (NEP) to latitude, for instance in
grasslands versus streams: NEP decreases significantly with latitude in grasslands, while
it increases in streams (Fig. 7d), a pattern confirmed with discrete climatic zones when
comparing mean NEP of these systems in arctic and tropical zones (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 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 multi-dimensional 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 uptake nutrients in soils and access to light (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 smaller producers than in those having large ones (e.g., forests versus stream in Table S3.4), in line with the metabolic theory of ecology (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’ 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 (Fig. 5c; e.g., between forest and pelagic marine ecosystems 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 mineralisation (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 (Fig. 5d), as previously found for different community types (Hatton et al., 2015); the regression slope lower than 1 on log-log scale indicates, however, that mass-specific uptake rates decrease with biomass across ecosystems (Fig. 5e). This second relationship also holds with a surprising consistency within ecosystem types (Fig. 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 is 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 integrate not only differences in uptake efficiency but also in structural and stoichiometric differences. This likely explains much of the difference in stocks, fluxes and rates at the ecosystem scale (Allen, Gillooly, & Brown, 2005; Schramski et al., 2015). For instance,
Multivariate ecosystem functioning

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 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 Appendix S2),
functioning types emerge that we hypothesize are driven by both the dominant primary
producer categories (e.g., tree, grass, algae), 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 organisational 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 Figs. 7, S4.4 and Tables S3.3 and S3.8) as
predicted by the MTE (Brown et al., 2004; Clarke, 2006; Gillooly, Brown, West, Savage,
& Charnov, 2001), and in line with the quite 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 Figs. 7 and 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 (Fig. 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 (Fig. 7d, Table S3.8), and between temperate and arctic lakes (Table S3.9). In fact, by slowing down detritivore activity (ER), cold temperatures make freshwater 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 Tables S3.1–S3.3) but not in a systematic way across ecosystem types (Figs. S4.3, S4.6, Table S3.8). Environmental constraints which 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, Yuan, Zhang, Tang, & Chen, 2011). For instance, drought limits more GPP than 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 investigate. 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 (Fig. 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 matter transformation should allow to compare the responses to perturbations of different ecosystem types and to identify testable mechanisms for potential variations. In that 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 (Fig. 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 evaluating 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
Multivariate ecosystem functioning

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, doi: 10.5281/zenodo.3644247. R scripts to reproduce the figures and statistical results are available.

Supporting information

Additional Supporting Information may be found online in the supporting information tab for this article.
**Figures**

**Figure 1 | Study design.**

- **a)** Ecosystem functioning variables considered in the study for each Ecosystem type x 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 gathered 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, ER, and U stand for Gross Primary Production, Ecosystem Respiration, and Uptake rate, respectively. 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.
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 @ naturalearthdata.com.
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, c and h). Boxplots give median (white line), 25% and 75% percentiles (box), extended by 1.5* inter-quartile range (whiskers). Scales were adapted to maximise clarity. For that purpose, 3 very low values of NEP in tropical streams and 5 null values of GPP in temperate streams and an aphotic benthic site are not displayed here (but see figure 7). Tables S3.11 and S3.12 of Appendix S3 in Supporting Information report the numbers of values of each Variable x Ecosystem type x Climatic zone combination, and the groups given by non-parametric post-hoc test of multiple mean comparisons within each variable, following a significant Kruskal-Wallis test (see methods).
**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, GPP, and ER stand for Net Ecosystem Production, Gross Primary Production and Ecosystem Respiration, respectively.

- **b** Stocks (Biomass, Organic carbon, 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 Tables S3.1, S3.2 and S3.6.
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 and ER stand for gross primary production and ecosystem respiration, respectively. 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 x climatic zone combination (see methods and 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 into brackets. 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 relations from bootstrap procedure between other pairs of ecosystem variables in Fig. S4.1, and correlations for subsets of empirical data for which pairs of variables are available per site in Table S3.13, Figs S2.10 and S2.11, and Appendix S2.4 for discussion.
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 x climate x variable combinations. Note that in each category, variables are pooled and not summed because it would be only meaningful for stocks. Then each variable has the same weight within each category of stocks, fluxes or rates. For purpose of clarity, scaled median values are double square root-transformed.
Regression lines for significant correlations between latitude and a gross primary production (GPP), b ecosystem respiration (ER), c decomposition rates (log-transformed values) or d net ecosystem production (NEP) and latitude, 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 Table S3.8). Significant correlations of stocks, uptake rates, and GPP/ER ratios with latitude are available in Figs. S4.3, S4.4 and S4.5, respectively.
List of Supplementary items in the Supporting information

(See new section after page 134, at the end of this file)

Appendix S1 Extended methods

Table S1.1 Definitions of ecosystem and climate categories
Table S1.2 Factors used for conversions into grams of carbon
Figure S1.1 Decision tree of the data collection process
Figure S1.2 Data treatment

Appendix S2 Data set presentation

Figure S2.1 Geographical distribution of data for each ecosystem variable
Figure S2.2 Data distribution among studies, sites, and ecosystem variables
Figure S2.3 Partitioning of biomass data
Figure S2.4 Comparing data with or without aboveground-only biomass estimates
Figure S2.5 Comparing freshwater data with or without partial biomass estimates
Figure S2.6 Methods used to estimate GPP in our data set
Figure S2.7 Boxplots comparing data with or without correction of estimates from $^{14}$C method
Figure S2.8 Functioning type gradient including correction for $^{14}$C method
Figure S2.9 GPP/ER ratios
Figure S2.10 Correlations among pairwise ecosystem variables (I – fluxes & rate)
Figure S2.11 Correlations among pairwise ecosystem variables (II – among stocks)

Appendix S3 Statistical results

Table S3.1 Two-way ANOVAs on ecosystem variables
Table S3.2 Two-way ANOVAs on broad categories of ecosystem variables
Table S3.3 Non-parametric tests for climatic effect on ecosystem variables
Table S3.4 Non-parametric tests for ecosystem type effects on ecosystem variables
Table S3.5 Non-parametric tests of mean differences among E x C combinations
Table S3.6 One-way ANOVAs on fluxes and rates of each ecosystem type
Table S3.7 Non-parametric tests on fluxes and rates of each ecosystem type
Table S3.8 Correlations between ecosystem variables and
Table S3.9 Non-parametric tests for climatic effect on NEP of each ecosystem type
Table S3.10 Non-parametric tests for climatic effect within forests
Multivariate ecosystem functioning

822 Table S3.11 Mean values, coefficients of variation and number of data points
823 Table S3.12 Non-parametric tests of mean differences among E x C combinations
824 Table S3.13 Empirical relationships between pairs of ecosystem variables
825
826 Appendix S4 Supplementary figures
827 Figure S4.1 Relationships between ecosystem variables
828 Figure S4.2 Principal Component Analysis (PCA) on median ecosystems
829 Figure S4.3 Latitudinal trends in ecosystem stocks
830 Figure S4.4 Latitudinal trends in mass-specific uptake rates
831 Figure S4.5 Latitudinal trends in GPP/ER ratios
832 Figure S4.6 Functioning shift of forests among climatic zones
833
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Global quantitative synthesis of ecosystem functioning
across climatic zones and ecosystem types

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Supporting Information

Content

Appendix S1 Extended methods ................................................................. 3
  Table S1.1 Definitions of ecosystem and climate categories.......................... 8
  Table S1.2 Factors used for conversions into grams of carbon........................ 9
  Figure S1.1 Decision tree of the data collection process................................ 10
  Figure S1.2 Data treatment........................................................................ 11

Appendix S2 Data set presentation ............................................................... 12
  Section S2.1 Geographical location .......................................................... 12
  Section S2.2 Data set structuration among studies and sites ....................... 12
  Section S2.3 Data set composition and variance ........................................ 12
  Section S2.4 Correlations between pairs of ecosystem variable: bootstrap versus site-level data 15
  Figure S2.1 Geographical distribution of data for each ecosystem variable .......... 17
  Figure S2.2 Data distribution among studies, sites, and ecosystem variables .... 18
  Figure S2.3 Partitioning of biomass data .................................................. 19
  Figure S2.4 Comparing data with or without aboveground-only biomass estimates .... 20
  Figure S2.5 Comparing freshwater data with or without partial biomass estimates .... 21
  Figure S2.6 Methods used to estimate GPP in our data set ......................... 22
  Figure S2.7 Boxplots comparing data with or without correction of estimates from $^{14}$C method 23
  Figure S2.8 Functioning type gradient including correction for $^{14}$C method .......... 24
Supporting information: Multivariate ecosystem functioning

**Figure S2.9** GPP/ER ratios ................................................................. 25
**Figure S2.10** Correlations among pairwise ecosystem variables (I – fluxes & rate) ............ 26
**Figure S2.11** Correlations among pairwise ecosystem variables (II – among stocks) ....... 27

**Appendix S3** Statistical results ................................................................. 28
  **Table S3.1** Two-way ANOVAs on ecosystem variables ........................................ 28
  **Table S3.2** Two-way ANOVAs on broad categories of ecosystem variables ................. 29
  **Table S3.3** Non-parametric tests for climatic effect on ecosystem variables ............... 30
  **Table S3.4** Non-parametric tests for ecosystem type effects on ecosystem variables ....... 31
  **Table S3.5** Non-parametric tests of mean differences among E x C combinations ........... 32
  **Table S3.6** One-way ANOVAs on fluxes and rates of each ecosystem type ................. 33
  **Table S3.7** Non-parametric tests on fluxes and rates of each ecosystem type ............... 34
  **Table S3.8** Correlations between ecosystem variables and latitude ........................ 35
  **Table S3.9** Non-parametric tests for climatic effect on NEP of each ecosystem type ...... 37
  **Table S3.10** Non-parametric tests for climatic effect within forests ......................... 38
  **Table S3.11** Mean values, coefficients of variation and number of data points ............. 39
  **Table S3.12** Non-parametric tests of mean differences among E x C combinations ........ 40
  **Table S3.13** Empirical relationships between pairs of ecosystem variables ............... 41

**Appendix S4** Supplementary figures ......................................................... 43
  **Figure S4.1** Relationships between ecosystem variables ...................................... 43
  **Figure S4.2** Principal Component Analysis (PCA) on median ecosystems ................... 44
  **Figure S4.3** Latitudinal trends in ecosystem stocks .......................................... 45
  **Figure S4.4** Latitudinal trends in mass-specific uptake rates ............................... 46
  **Figure S4.5** Latitudinal trends in GPP/ER ratios ............................................. 47
  **Figure S4.6** Functioning shift of forests among climatic zones ............................ 48

**Appendix S5** Supplementary references ..................................................... 49
Appendix S1 – Extended methods

This appendix provides details on the methods used in this study.

Data collection

Our systematic search covered four broad categories of terrestrial ecosystems (forest, grassland and shrubland, agroecosystem, and desert) and four of aquatic ecosystems (stream, lake, pelagic ocean, and benthic ocean). We considered all ecosystems (if available) in five major global climatic zones (arctic/alpine, boreal, temperate, tropical, and arid). Table S1.1 provides the definitions of ecosystem categories and climatic zones. For marine ecosystems, we grouped arctic, boreal, and temperate versus arid and tropical climates into Cold and Warm, respectively, to account for a lesser influence of climate on oceanic systems due to the buffering effect of large water volumes. For each relevant ecosystem x climatic zone combination, we collected data of carbon stocks (biomass, organic carbon, detritus), fluxes (gross primary production (GPP), ecosystem respiration (ER), and net ecosystem production (NEP)), and rates (uptake and decomposition rates) (see Fig. 1). We used all possible combinations of these categories and terms with similar meanings (see Table S1.1) in our systematic search. A first systematic search was conducted by using all possible combinations of the names of each ecosystem type, climatic zone and ecosystem variable of interest, with small variation when relevant (e.g. “decomposition OR decay” for decomposition flux and rates). The different terminologies used across various research fields to describe the same processes, and the fact that the data of interest were often located in different sections of the studies (Methods versus Results) limited the efficiency of standardized keyword search across the data types. We therefore complemented the dataset with multiple customized searches until we compiled a minimum number of ten independent values of each variable of interest (i.e. different stocks, fluxes, and decomposition rate) for each ecosystem x climatic zone combination. Figure S1.1 shows the flow of this recursive process and the associated decision tree to integrate studies in the data set. Our aim was not to be completely exhaustive but rather to provide representative ranges of variation for the different ecosystem variables. In total, we collected 4,479 values from 604 published studies (this count does not include the 512 GPP/ER ratios provided in the data table).

Calculations used for data extraction

When only one or two of three major fluxes (gross primary production, ecosystem respiration, and net ecosystem production (GPP, $R_e$, and NEP, respectively) were reported, we estimated the unreported flux:

\begin{align*}
\text{NEP} &= \text{GPP} - \text{Re} \quad [1] \\
\text{NEP} &= \text{NPP} - \text{Rh} \quad [2] \\
\text{NPP} &= \text{GPP} - \text{Ra} \quad [3]
\end{align*}
NPP is the net primary production, $R_h$ the heterotrophic respiration, and $R_a$ the autotrophic respiration. The ratio GPP/R_e was also calculated to compare with the NEP data (see Appendix S2.3).

Uptake rates were rarely reported as such. Some relative growth rates (RGR) were documented, but often at species and not community level only and as instantaneous maximal values (potential growth). Since we wanted to analyse uptake rates relevant at the ecosystem level and at yearly timescale, we thus looked at studies reporting both GPP and biomass of autotrophs, $B_a$, at the same sites and calculated community uptake rates $U$:

$$U = \frac{\text{GPP}}{B_a} \quad [4]$$

As measures of decomposition rates, we collected values of $k$, the first order constant in the classical exponential decay model:

$$D_F = D_M(1 - e^{-kt}) \quad [5]$$

with $D_F$ the decomposition flux and $D_M$ the detritus stock. When not directly provided, we derived $k$ with one of the equations proposed by (Cebrian & Lartigue, 2004) depending on the data available in the study:

$$D_t = D_{t_0} e^{-k(t-t_0)} \quad [6]$$

$$D_F = (D_P - E)(1 - e^{-kt}) \quad [7]$$

In Equation [6], $D_t$ is the detrital mass at time $t$ and $D_{t_0}$ the initial detrital mass. This equation was used when decomposition was estimated as the proportion of detrital mass loss ($1 - D_t/D_{t_0}$) via a litter-bag experiment, a classical method in freshwater and terrestrial ecology. In equation [7], $D_F$ is the (absolute) decomposition flux during the study period $t$, that is the flux from detritus stock to bacteria and other detritivores, $D_P$ is the detritus production, and $E$ the detritus export (e.g. sedimentation). In few cases of ocean pelagic data, we used the microbial loop of primary production versus bacterial production to parameterize $D_P$ and $D_F$, respectively. If not available, the export rate was set to 0, leading to $k$ underestimation, which is conservative in our cross-ecosystem comparison given that $k$ is already at the higher end of the range in these pelagic systems.

**Unit conversions**

Once collected, we standardized values by converting them all into areal carbon units, that is, gC m\(^{-2}\) for stocks, and gC m\(^{-2}\) yr\(^{-1}\) for fluxes, and g g\(^{-1}\) yr\(^{-1}\) for mass-specific uptake rates, and yr\(^{-1}\) for decomposition rates. Figure S2.2 details this data processing.

**Carbon conversion:** We used data in carbon units (gC) when it was directly provided in the study, or we calculated the values using carbon content when reported in the study (79% of data points). Alternatively, we converted the data into carbon units using the most specific conversion factor available depending on the level of detail about the material of interest (see Table S1.2 for conversion factors). For uptake rates, mass-normalization often made conversions unnecessary. Data were converted for calculations to homogenize units of GPP and autotrophic biomass when needed. For decomposition rates, we did not transform units into carbon. We made the most parsimonious assumption that carbon loss rate is identical to loss rate in the unit provided (generally
dry weight or ash-free dry weight). While this is a simplification, we concluded that this best allowed us to keep measurements consistent across data sources, in the absence of more detailed information.

**Time extrapolation:** 65% of local fluxes or rates were already provided in yearly units. For the others, we extrapolated to the year by using the number of days in the growing season as reported in the study, or the ice-free period in cold climates. When growing season length (GSL) was not specified in the study we used averaged estimates detailed by Garonna et al. (2014) for the different climatic zones in Europe (Mücher, Klijn, Wascher, & Schaminée, 2010): 181 days for temperate climate (mean of “atlantic” and “continental”), 155 days for boreal, 116 days for arctic, and 163 days for arid systems (mean of “Mediterranean” and “steppic”). We assumed no strong seasonality in tropical climates (365 days of GSL). We did not apply any conversion if the value was measured on a study period longer than the above GSL for the corresponding climate.

**Volume to area conversions and depth integration:** Some data were given per unit of volume. For freshwater systems, we converted the data into area units by integrating them over the water column, using the mean depth of the river or lake. When not directly available in the study we calculated depth by dividing the volume per the area in lakes, or by estimating depth from discharge in rivers with the formula depth = \(c \times Q^f\), with \(c = 0.2\), \(f = 0.4\) and \(Q\) the discharge in m\(^3\) s\(^{-1}\) (see Rodriguez-Iturbe & Rinaldo (1997)). For small catchment areas, that is <1 km\(^2\), we estimated the depth to be 5 cm based on known river scaling-properties (Rodriguez-Iturbe & Rinaldo, 1997). For marine data, notably production in the pelagic zone, studies generally provide a meaningful depth, which defines the euphotic zone such as the Secchi depth or the 1% light inflow depth. We integrated values in volume units over this depth, and to 100 m depth when only sampling depths were provided. For terrestrial and benthic marine ecosystems, carbon in soils or sediments was standardized by integrating it over the thirty first centimetres.

**Statistical analyses**

Firstly, we performed two-way analyses of variance (ANOVA) to determine the contribution of ecosystem type E and climatic zone C in explaining the variance within each ecosystem variable and within broad categories of variables, that is, stocks, fluxes and rates (see Methods in main text for details on broad categories, Fig.4, Tables S3.1, S3.2). The linear model used was \(y \sim C + E + C:E\), with \(y\) being one of the seven ecosystem variables. Since variances were not homogenous, we performed non-parametric Kruskal-Wallis tests on ranks for multiple mean comparisons to test the mean differences among climatic zones (Table S3.3), among ecosystem types (Table S3.4), and climatic zone x ecosystem type combinations (Table S3.5). Results between parametric and non-parametric tests were identical. We analysed further climatic influence on GPP, ER and decomposition rate within each ecosystem type (excluding deserts and agro-ecosystems which are represented only in one climatic zone). We performed both one-way ANOVAs (Table S3.6) and non-parametric Kruskal-Wallis tests on ranks (Table S3.7), on those 18 ecosystem variables x ecosystem type combinations, with climatic zone as explanatory variable. For all the above analyses we used the initial five categories of climatic zones (i.e., arctic. boreal. temperate. tropical and arid),
but we also performed the non-parametric tests adding the pooled categories “Warm” (i.e., tropical + arid) and “Cold” (i.e., arctic, boreal, temperate) for marine systems to provide the groups corresponding to the figure displaying the data (Fig. 3; Table S3.12). After each Kruskal-Wallis test, we performed a post-hoc test of multiple comparisons on rank sums to get the groups. For that we performed a Dunn’s test using the dunn.test R-package (Dinno, 2017).

Secondly, we analysed the covariance between pairs of ecosystem variables across ecosystem types. We used a bootstrapping procedure to include the variance present in our data despite independent origins between ecosystem variables (see Methods in main text for more details on this procedure). We performed two-sided Pearson’s correlation tests on the set of 10,000 bootstrapped data for each pair of ecosystem variables. 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. In addition, we visualize the variability by showing both the standard deviation of ecosystem variables’ distributions (bars in Fig. 5, Fig. S4.1) and the 95% confidence interval (CI) derived from linear regressions made on the series of bootstrapped values (shaded areas). CIs were calculated for 1,000 values along the x-axis, for which we recorded the y-values predicted by each of the 10,000 linear regressions; the boundaries of the shaded area correspond to the 95% confidence interval of the y-values distributions along x-axis. Figures also show the ‘mean’ regression line defined by the mean slope and intercept (Fig. 5, Fig. S4.1). Note that we minimized the sum of orthogonal distances to the line rather than of residuals squares in these linear regressions to avoid side bias (we do not assume that one of the two variable explains the other one). Furthermore, we carried out a Principal Component Analysis (PCA) on median values of the variables in each E x C combination to examine the relative position of ecosystems in the space defined by all individual ecosystem variables (see Fig. S4.2). We corroborated our general findings by performing correlation tests on the subsets of data for which pairs of variables were available per site (see discussion in Appendix S2 section S2.4, Figs S2.10 and S2.11, and Table S3.13).

Thirdly, we analysed the correlations between ecosystem variables within each ecosystem type and latitude, using two-sided Pearson’s correlation tests. In Table S3.8, we report the results of all these tests, along with slopes and intercepts of the corresponding linear regressions when the test was significant.

Software

We analysed the data and plotted the figures with the open source software R version 3.6.1 (R Core Team, 2019) and different R-packages:

- Figure 1 (to show the map): maps (Becker & Wilks, 2018)
- Figures 5 and S4.1: vioplot (Adler, 2018) to show the distribution of correlation coefficients, minpack.lm (Elzhov, Mullen, Spiess, & Bolker, 2016) for the linear regression and, ade4 (Dray & Dufour, 2007) to add a scatter plot;
- Figure 6: plot3D (Soetaert, 2017);
- Figure S4.2: FactoMineR for the PCA (Le, Josse, & Husson, 2008);
- Statistical tests: pgirmess (Giraudoux, 2018) (post-hoc tests of multiple mean comparison on rank sums), dunn.test (Dinno, 2017) (post-hoc test of multiple mean comparison on rank sums), multcompView (Graves, Piepho, Selzer, & with help from Dorai-Raj, 2015)(to find the groups);
- Figure S2.2: RColorBrewer (Neuwirth, 2014) for the colours.

Final artwork was realized with Illustrator CC 22.0.1.
<table>
<thead>
<tr>
<th>Climates zones</th>
<th>Definition</th>
<th>Example ecosystems</th>
</tr>
</thead>
<tbody>
<tr>
<td>Arctic</td>
<td>Extreme temperature limitation of growing season length, with abiotic conditions not supporting tree growth in arctic, subarctic, and alpine zones; OR high latitude oceans, generally above 66.5°</td>
<td>Tundra (grassland), Alpine grassland</td>
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<tr>
<td></td>
<td>Strong temperature limitation of terrestrial growth, but environment supports tree growth. Covers northern parts of North America, Europe, and Russia from latitudes 50° to 55°; OR oceans between 50° and 66.5°</td>
<td>Taiga (forest), Sub-alpine forest</td>
</tr>
<tr>
<td>Temperate</td>
<td>Seasonal terrestrial growth with some temperature limitation. Covers latitudes between 23.5° and 50° to 55°, including oceans in this latitudinal range</td>
<td>Beech forest</td>
</tr>
<tr>
<td>Tropical</td>
<td>Warm terrestrial tropical, sub-tropical, equatorial systems not limited by drought between 0° to 23.5° latitude (including subtropical system), including oceans in this latitude range</td>
<td>Savanna (grassland), rainforest</td>
</tr>
<tr>
<td>Arid</td>
<td>Severely water-limited terrestrial systems at all latitudes, including arid, semi-arid, xeric, xerophytic, xeromorphic, Mediterranean systems, continental, warm or cold, and polar deserts</td>
<td>Garrigue (grassland), shrubland (grassland or forest, depending on the canopy), chaparral (grassland), steppe (grassland), caatinga (forest), cerrado</td>
</tr>
<tr>
<td>Ecosystems</td>
<td>Definition</td>
<td>Example ecosystems</td>
</tr>
<tr>
<td>Forest</td>
<td>Complete vegetation cover with trees as dominant vegetation; tree canopy covers most of the surface</td>
<td>Rainforest, caatinga, woodland, some shrubland, cerrado</td>
</tr>
<tr>
<td>Grassland and shrubland</td>
<td>Complete vegetation cover, but with only very few or no trees; vegetation dynamics dominated by water limitation, fires, and grazing.</td>
<td>Steppe, savannah, meadow, prairie, tundra, old field, some shrublands, herbaceous rich-fen vegetation</td>
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<tr>
<td>Desert</td>
<td>Extreme growth limitation by water availability. With little vegetation distributed in remote patches</td>
<td>Sandy land</td>
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<tr>
<td>Agro-ecosystem</td>
<td>Ecosystems devoted to crop production or cattle grazing, often fertilized or irrigated to remove nutrient or water limitations for growth</td>
<td>Cropland, pasture, field, vineyard, orchard</td>
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<tr>
<td>Stream</td>
<td>Running freshwater and lotic systems of all sizes, including rivers</td>
<td>Creek, brook, river, stream</td>
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<tr>
<td>Lake</td>
<td>Standing (lentic) freshwater systems</td>
<td>Reservoir, lake, pond</td>
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<tr>
<td>Ocean</td>
<td>All salt water ecosystems with no emerged vegetation, including internal seas</td>
<td>Sea, ocean shelf, estuary, lagoon</td>
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<tr>
<td>Ocean pelagic</td>
<td>Ecosystems in the open water columns of oceans and seas</td>
<td>Upwelling system, open ocean</td>
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<tr>
<td>Ocean benthic</td>
<td>Ecosystems at the bottom of oceans and seas</td>
<td>Coral reef, sea grass bed, eelgrass meadow, kelp forest, deep-sea flour</td>
</tr>
</tbody>
</table>
**Table S1.2 | Factors used for conversions into grams of carbon.**

KJ = kilojoule; Kcal = kilocalorie; mol C = mole of carbon; g CO₂ = gram of carbon dioxide; g O₂ = gram of di-oxygen; mol O₂ = mole of di-oxygen; g WW = gram of wet weight; g DW = gram of dry weight; g AFDW = gram of ash-free dry weight. Values into brackets give the percentage of raw values converted using a given factor.

<table>
<thead>
<tr>
<th>Type of material</th>
<th>KJ</th>
<th>Kcal</th>
<th>mol C</th>
<th>g CO₂</th>
<th>g O₂</th>
<th>mol O₂</th>
<th>g Chla</th>
<th>g WW</th>
<th>g DW</th>
<th>g AFDW</th>
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<tbody>
<tr>
<td>Organic Tissue *</td>
<td>0.02</td>
<td>0.09</td>
<td>12</td>
<td>0.2727</td>
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<td>0.09</td>
<td>0.45</td>
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<td>(0.08%)</td>
<td>(0.10%)</td>
<td>(3.01%)</td>
<td>(2.46%)</td>
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<td>(0.94%)</td>
<td>(2.70%)</td>
<td>(4.39%)</td>
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<td>Productivity, photosynthetic quotient = 1.2 b</td>
<td>0.3125</td>
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<td>(3.33%)</td>
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<td>Respiration, respiratory quotient = 1ab</td>
<td>0.375</td>
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<td>Non-woody primary producer terrestrial c</td>
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<td>(3.11%)</td>
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<td>Algae, sea grasses c</td>
<td>50</td>
<td>1/16.7</td>
<td>1/2.92</td>
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<td>(0.76%)</td>
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<td>Arthropods d</td>
<td>0.496</td>
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* from Table 1 p26 in Weathers, Strayer, & Likens (2013), and references therein.

b from supplementary references: Duarte et al., (2010); Huchette, Beveridge, Baird, & Ireland (2000); Irons III & Oswood (1997).

c from Table 2.5 p26 in Opitz (1996) for conversions factor from WW and DW; Conversion factor for Chl-a from Peterson, Hobbie, & Corliss (1986).

d from Small, Torres, Schweizer, Duff, & Pringle (2013).

* used general conversion factor 0.45 for DW in deserts and arid grasslands where the vegetation includes woody species.
Figure S1.1 | Decision tree of the data collection process.

Steps 1, 2, 10, 12 describe the recursive steps of data search. Steps 3 to 9 describe the decision tree to include or not a paper in our collection.
Figure S1.2 | Data treatment.

Conversions applied to raw value to homogenize units to g C m$^{-2}$, g C m$^{-2}$ yr$^{-1}$, and yr$^{-1}$, for stocks, fluxes, and rates, respectively. Percentage refer always to the whole data set. Notes: 1 Some lake mean depths were found elsewhere when not provided in the study. 2 We estimated river mean depth with discharge and lake mean depth with area and volume when not directly provided. 3 Secchi or 1% light attenuation depths were used to integrate biological fluxes and stocks when provided. 4 GSL: Growing Season Length. 5 mean GSL values used to standardize: 116, 155, 163, and 181 days for arctic, boreal, arid, temperate climatic zones, respectively (see explanations and references in Appendix S1).
Appendix S2 – Data set presentation

This appendix presents the data set, relevant information on its content and on some identified possible sources of variability, to facilitate a nuanced interpretation of the observed patterns.

S2.1 Geographical location

Data are spread over the world (Fig. 2), with a typical under-representation of the southern hemisphere, notably for terrestrial and freshwater ecosystems. This tendency is illustrated by deserts, for instance, which are mainly represented by North American and Chinese deserts, and almost no data for African ones. Partitioning of individual variables shows no obvious geographical clustering (Fig. S2.1).

S2.2 Data set structuration among studies and sites

Half of the studies consider a single site, and less than 15% of the studies consider more than five sites (Fig. S2.2a, b). Similarly, most studies (46%) focus on a single ecosystem variable, while 34% of the studies consider two to three variables (Fig. S2.2c, d), which was often either several fluxes or several stocks; since a special collection effort was made on finding papers which provide both GPP and autotrophic biomass to estimate uptake rates, biomass is also recurrently found with flux data in our data set. The 15% studies considering more than four ecosystem variables are often studies on single sites, mostly aquatic ones, with a whole ecosystem budget perspective. This includes, for instance, studies on carbon budget in freshwater ecosystems, or studies gathering estimates to feed ECOPATH models in marine or lake ecosystems. Overall, we most often have only one ecosystem variable estimate per site (56%), which justified our bootstrapping approach to examine pairwise variable correlations (Figs. 5 and S4.1). For example, estimates of decomposition rates come mostly from decomposition experiments which do not provide any of the other focal variables we are considering here. By contrast, some variables are almost systematically measured together at the same site, such as GPP and ecosystem respiration (491 data points), biomass and detritus (213 data points), or biomass and GPP due to our search of uptake rate estimates (252 data points). Tables S3.13 and figures S2.10 and S2.11 display the significant correlations tests for available pairs of variables at the site-level (see also section S2.4 below).

S2.3 Data set composition and variance

Variance in our data set comes from both natural variation among and within the ecosystems looked at, and diversity and variability in what was measured and how (i.e. variation caused by the measurement and methods). These two levels of variation cannot be separated in our data set but we here discuss the individual components of our study (stocks, fluxes, and rates), their respective specificities with respect to data origin and specific possible biases. Coefficients of variation for each ecosystem variable are provided in Table S3.11.
**Biomass**

Biomass represents different components of the ecosystem depending on ecosystem type. Available estimates are most often representative for the organisms contributing the most to the biomass. In terrestrial ecosystems, or in benthic ecosystems such as dense seagrass beds or kelp forests, primary producers constitute most of the biomass (see Fig S2.3). In this case, methods are relatively standard (harvesting), but we gathered aboveground-only (A) and above+belowground (AB) estimates, which adds to natural variation (Fig S2.3b). Omitting roots necessarily underestimates biomass in terrestrial ecosystems, however, biomass increases significantly only in tropical forests when removing aboveground-only data (Fig. S2.4). In aquatic ecosystems, biomass also integrates heterotrophs (Fig S2.3b), especially when not dominated by macroalgae. In freshwater ecosystems, biomass measurements of the whole community are rare and estimates are often epilithon or macroinvertebrate-only data without fish. We thus acknowledge that at least half and a quarter of the data, for streams and lakes respectively, are obvious underestimations (Fig S2.3c). However, removing these partial data gives significantly higher mean biomass only in tropical streams (Fig S2.5). Overall, despite variability in the biomass estimates, we are confident that the strong among-ecosystem differences we observe are robust to those differences in documented biomass.

**Organic carbon**

Storage of decomposed organic carbon differs fundamentally in terrestrial-benthic versus freshwater-pelagic ecosystems. The estimates for the former are carbon stored in the first 30 cm of soils or sediments and reach areal amounts of magnitudes 1000–10,000 g m\(^{-2}\). For the latter, estimates are organic carbon dissolved in the water column and range three to four orders of magnitude lower. Methods for both types of measurement are highly standardized and variance likely reflects the natural variation.

**Detritus**

Detritus is the ecosystem variable showing on average the highest coefficients of variation (Table S3.11). In terrestrial and macroalgae-dominated ecosystems detritus is most often the litter layer, sometimes also including dead standing stock. In freshwater ecosystems, detritus is not only autochthonous detritus but also detritus from terrestrial riparian systems in the form of fine or coarse particulate matter, and sometimes woody debris. Differences in adjacent terrestrial land use thus partly explain a high variance in freshwater detritus. In pelagic marine systems, detritus is particulate organic matter, which is either locally produced in the open ocean, or a combination of locally produced particulate organic matter and organic matter inflow from freshwater systems in estuaries. Sedimentation and fast decomposition through the microbial loop keep detritus stocks at low levels in the water column of these systems.
**Ecosystem fluxes**

The methods to measure ecosystem fluxes vary strongly among ecosystem types (Fig. S2.6). Notably, in terrestrial systems, CO$_2$ fluxes are mainly measured with the Eddy-covariance method from flux towers or chambers equipped with portable infrared gas analysers (73% of GPP estimates), but also satellite data (11% of GPP estimates; MODIS: MOderate Resolution Imaging Spectrometer) or more traditional methods involving the budget of biomass increment of plants (NPP) and autotrophic respiration (9%). In freshwater and benthic marine ecosystems, the dominant methods to estimate of photosynthesis and respiration are based on change of dissolved oxygen concentration in time or space (83% of GPP estimates), while in pelagic marine systems, incorporation of $^{14}$C into the biomass is the preferred method to estimate primary production (62%). This last method, however, gives estimates that lie between GPP and NPP depending notably on incubation time (Codispoti et al., 2013). To assess that this was not affecting our conclusions, we identified data which were estimated from this method with an incubation time longer than 6H or unknown (to be conservative), and were likely to underestimate GPP. This concerns 47/687 estimates of GPP and 18/309 of uptake rates (calculated from local GPP and producer biomass). We applied a factor of 0.5 to these estimates, which is also very conservative according to some studies providing both NPP and GPP (e.g., factor of 0.88 in Carstensen, Conley, & Müller-Karulis (2003)), and re-run the analyses. This obviously has some quantitative effect, for instance lowering the strength of the relationship between latitude and GPP but increasing the one with uptake rates in pelagic marine systems, or increasing the strength of the correlations observed in Fig5b, 5d and 5e between pairs of ecosystem variables. Importantly, the general qualitative cross-ecosystem differences and the gradient of ecosystem functioning still hold (Figs. S2.7 and S2.8). Thus, while there are differences in the technical approaches how ecosystem fluxes are assessed, these differences do not change the qualitative relationships documented here.

**NEP versus GPP/ER**

NEP, shown in figure 3f, is a classical metric to assess ecosystem heterotrophy. However, differences in methodologies to measure GPP and ER can inflate errors when calculating NEP and might skew cross-ecosystem comparisons (Honti & Istvánovics, 2019). We therefore also examined the GPP/ER ratio, which removes such potential biases (Fig. S2.9). These latter ratios confirm the global trends in ecosystem heterotrophy with values generally above one in terrestrial and pelagic systems (78%) and often below one in freshwater and benthic ecosystems (78% also). Significant differences among climatic zones are identical for GPP/ER ratios and NEP (Table S3.3). GPP/RE also increases significantly with latitude in streams, while the weak negative correlation found for NEP in grasslands disappears (Table S3.8 and Figure S4.5). General differences among ecosystem types are also confirmed, although slightly weaker than for NEP (Table S3.4).
**Carbon uptake rates**

The vast majority of our carbon uptake rate estimates is calculated from studies where both GPP and autotrophic biomass was provided. In terrestrial ecosystems, uptake rates might be slightly overestimated when only aboveground biomass is considered, while in aquatic ecosystems potential overestimations due to methods to estimate primary production (see above) did not lead to significant differences in mean uptake rates (Fig. S2.7). Our results are thus conservative regarding the higher uptake rates in aquatic compared to terrestrial ecosystems.

**Decomposition rates**

Decomposition rates are most often obtained from litter bag experiments in terrestrial, freshwater and benthic ecosystems. In terrestrial and benthic ecosystems, the litter used comes from the same type of ecosystem, often comparing the local decomposition of different leaf species found regionally, while in freshwater ecosystems litter is of terrestrial origin. Thus, differences between terrestrial and freshwater decomposition rates reflect mostly differences in physical factors and decomposer communities. It’s likely that decomposition of autochthonous production would increase estimate values in freshwater ecosystems because aquatic primary producers are way more labile than terrestrial ones (Elser et al., 2000). The observed differences are therefore conservative. Variations in decomposition rates among litter types of different species contribute a lot to within-ecosystem variations.

Estimates for pelagic marine ecosystems were not easy to find and the variability of our values also reflects strong methodological heterogeneity: Decomposition of local production was often estimated by the microbial loop, notably in the open ocean: that is the ratio of bacteria to phytoplankton production, in other words the production processed by bacteria (e.g., Cho & Azam, 1988; Ducklow, 1999; Kirchman, Keel, Simon, & Welschmeyer, 1993). Our data set integrates also estimates from measurements of remineralization rates of dissolved or particulate organic carbon (e.g., Gan, Wu, & Zhang, 2016), which gives lower values than the bacterial loop, or from a classical decomposition experiment on salp carcasses (an important component of zooplankton in some places), which gave us a high-value outlier (Stone & Steinberg, 2016).

**S2.4 Correlations between pairs of ecosystem variable: bootstrap versus site-level data**

To examine the relationships between ecosystem variables we adopted a bootstrapping strategy (see Methods and Appendix S1) due to the low number of per-site data for some pairs of variables. For instance, despite very extensive targeted literature searches, we only found ten sites across all ecosystem types which had data to document both uptake and decomposition rates. Nevertheless, we also tested pairwise-variable correlations on subsets of our data set when estimates for both variables were provided (thereafter called ‘empirical’ correlations; see Table S3.13 for all significant correlations and figures S2.10 and S2.11). These empirical correlations support all the findings obtained from bootstrapped values. They also quantify some significant cross-ecosystem
relationships that are not indicated by our conservative bootstrap approach, for instance a negative relationship between detritus and decomposition, or positive relationships between ecosystem respiration and biomass or organic carbon (Table S3.13).

Additionally, correlation tests were performed within each ecosystem type for each ecosystem variable pair, which reveals whether relationships between variables emerge solely from cross-ecosystem differences or also from constraints operating at the ecosystem level. Notably, the positive relationship observed between biomass and organic carbon (Fig. 5a) clearly results from cross-ecosystem differences, with no within-ecosystem relationships detected (Fig. S2.10b), while the strong positive correlation between GPP and ER is also highly significant within each ecosystem type (Figs. 5b and S2.10d). This relationship is well-known and expected, notably in terrestrial ecosystems where ecosystem respiration is the sum of autotrophic respiration, which is causally connected with GPP, and heterotrophic respiration, which consists mostly in soil microbial respiration fed by plant detritus and exudates. Note, however, that this relationship is weaker and less systematically expected in aquatic ecosystems. In these ecosystems, respiration can result dominantly from the decomposition of allochthonous matter and be relatively disconnected from a low in-situ GPP (for example in rivers with high riparian cover or benthic ecosystems in deep or turbid water).

Interestingly, the strong negative relationship between ecosystem biomass and primary producer uptake rates holds both across and within ecosystem types (Fig. S2.10b). At cross-ecosystem level, the relationship likely emerges from contrasting differences among primary producers (e.g., size, composition in structural tissues), as discussed in the main text. Within ecosystems, the relationship can be interpreted as a result of both specific variation in producers and competition: higher biomass can result from more individuals which fix carbon at a lower rate due to mutual shading for instance.
Figure S2.1 | Geographical distribution of data for each ecosystem variable.

Each dot shows the geographic location of sites from which we obtained data. Colours denote the different ecosystem types. For about 13% of the data either the coordinates are not provided or the geographical scale given is either too large or too coarse to be meaningfully reflected in the map. The map is made with Natural Earth. Free vector and raster map data @ naturalearthdata.com.
Figure S2.2 | Data distribution among studies, sites, and ecosystem variables.

Histograms (a, c, e) and pies (b, d, f) of (a, b) number of sites per study, (c, d) number of ecosystem variables per study and (e, f) number of ecosystem variables per site. The eight ecosystem variables considered here are: biomass, organic carbon, detritus stocks, gross primary production, ecosystem respiration, net ecosystem production, and uptake and decomposition rates. Some of the estimates were not directly provided but calculated from data provided in the studies (see Appendix S1). This analysis considers the data of 599 of the in total 604 studies in the complete synthesis; data from five studies had to be excluded as they provided only biome-scale estimates.
**Figure S2.3 | Partitioning of biomass data.**

Panel a shows the percentage of biomass estimates representing only primary producers (P), only heterotrophs (H) or both primary producers and heterotrophs (P+H). Panel b shows the percentage of estimates of primary producer biomass that include only aboveground (A) or both above and belowground biomass (A+B) in terrestrial and marine benthic ecosystems. Panel c shows the percentage of biomass estimates which are assumed to represent the majority of community biomass (in dark; e.g. trees in forests) or which are known to be only a partial estimate (in light grey). Estimates of complete communities were difficult to found in freshwater ecosystems. Numbers of data points are provided on the top of each panel.
**Figure S2.4 | Comparing data with or without aboveground-only biomass estimates.**

Biomass data across different ecosystem types (left to right) and for different climatic zones (colours). Transparent colour boxes are for data from which we removed aboveground-only estimates of primary producer biomass while solid boxes are for the complete distribution. Points give values, with “x” denoting outliers. Zero values are replaced by 0.01 to be displayed despite log scales and are given as “+”. Boxplots give median (white line), 25% and 75% percentiles (box), extended by 1.5* inter-quartile range (whiskers). Numbers of data points (n) are given on the panel top. Only tropical forests show a significant difference, denoted by an asterisk) between data with or without aboveground-only data (Wilcoxon test W=364; p-value = 0.03).
Figure S2.5 | Comparing freshwater data with or without partial biomass estimates.

Biomass data across different ecosystem types (left to right) and for different climatic zones (colours). Transparent colour boxes are for data from which we removed the data that clearly underestimate biomass (e.g., invertebrate-, fish-, periphyton- or epilithon-only data). Points give values, with “x” denoting outliers. Boxplots give median (white line), 25% and 75% percentiles (box), extended by 1.5* inter-quartile range (whiskers). Numbers of data points (n) are given on the panel top. Only tropical streams show a significant difference, denoted by an asterisk) between data with or without partial biomass estimates (Wilcoxon test W=46.5; p-value < 0.001).
Figure S2.6 | Methods used to estimate GPP in our data set.

EC: Eddy-covariance methods; IRGA: Infrared Gas Analyser. MODIS: MODerate Resolution Imaging Spectrometer (satellite data); “Budget” refers to methods adding measures of autotrophic respiration and NPP estimates from biomass increment measures. “$^{14}$C short” refers to methods measuring the incorporation of $^{14}$C into biomass with incubation times up to 6 hours. “$^{14}$C long” refers to methods measuring the incorporation of $^{14}$C into biomass with incubation times higher than 6 hours, or when the incubation time is not specified (to be conservative). “Oxygen” refers to method based on change in dissolved oxygen concentration in time or space. “Models” refers to different empirical models (for instance involving the construction of chlorophyll-a – irradiance curves or outputs of ECOPATH models fed with empirical estimates). “Other” includes methods for instance measures of CO2 based on pH titration or measure of nutrient uptake.
Figure S2.7 | Boxplots comparing data with or without correction of estimates from $^{14}$C method.

GPP (top panel) and uptake rate data (bottom panel) across different ecosystem types (left to right) and for different climatic zones (colours). Transparent colour boxes are for data subsets in which estimates were divided by two when estimation involved the method of $^{14}$C incorporation with a long incubation time because the primary production estimation is thought to be then closer to net than to gross primary production (Codispoti et al., 2013). This concerns 47/687 values of GPP and 18/309 of uptake rates, mainly in ocean pelagic and arctic lake ecosystems. Points give values, with “x” denoting outliers. Zero values are replaced by 0.1 to be displayed despite log scales and are given as “+”. Boxplots give median (white line), 25% and 75% percentiles (box), extended by 1.5* inter-quartile range (whiskers). Numbers of data points (n) are given on the panel tops. Arrows highlight the decrease in median values. None of the Wilcoxon tests performed on pairs of corrected/not corrected data (individual pairs of solid and transparent boxplot) showed a significant mean difference, thus indicating that, overall, both qualitative and even quantitative differences due methodological differences in ecosystem flux measurement methods, have minor consequences on global patterns.
Figure S2.8 | Functioning type gradient including correction for $^{14}$C method.

Relative positions of median ecosystem 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 x climate x variable combinations. For purpose of clarity, scaled median values are double square root-transformed. Arrows and grey shapes show the new position of median ecosystems when a correction factor of 0.5 is applied on estimates of GPP and uptake rates which measurement involved the method of $^{14}$C incorporation with a long incubation time. In this case, primary production estimation is thought to be then closer to net than to gross primary production (Codispoti et al., 2013).
Figure S2.9 | GPP/ER ratios.

Ratios of gross primary production (GPP) to ecosystem respiration (ER) across different ecosystem types (left to right) and for different climatic zones (colours). Points give values, with “x” denoting outliers. Boxplots give median (white line), 25% and 75% percentiles (box), extended by 1.5* inter-quartile range (whiskers). Numbers of data points (n) are given on the panel top.
Figure S2.10 | Correlations among pairwise ecosystem variables (I –fluxes & rate).

Shapes show the data points in different climatic zones. Colours denote ecosystem types. Lines show regression lines for significant correlations between selected ecosystem variables in the different ecosystem types, based on two-sided Pearson’s correlation tests. Pearson correlation coefficients and p-values are provided for these significant relationships, with the number of data points in brackets (see legend for abbreviations of ecosystem types). “ER” and “GPP” stands for ecosystem respiration and gross primary production, respectively. Uptake rates are GPP values divided by autotrophic biomass. Dotted lines show regression lines for significant correlation tests performed on all the points (all ecosystem types). “Tot” reports the corresponding statistics.
Figure S2.11 | Correlations among pairwise ecosystem variables (II – among stocks).

Shapes show the data points in different climatic zones. Colours denote ecosystem types. Lines show regression lines for significant correlations between selected ecosystem variables in the different ecosystem types, based on two-sided Pearson’s correlation tests. Pearson correlation coefficients and p-values are provided for these significant relationships, with the number of data points in brackets (see legend for abbreviations of ecosystem types). Dotted lines show regression lines for significant correlation tests performed on all the points (all ecosystem types). “Tot” reports the corresponding statistics.
### Appendix S3 – Statistical results

**Table S3.1 | Two-way ANOVAs on ecosystem variables.**

Results of seven analyses of variance (ANOVA) performed on ecosystem variables with climatic zone (C) and ecosystem type (E) as explanatory variables; model: \( y \sim C + E + C: E \) (statistics for Figure 4a). NEP, GPP, and ER stand for net ecosystem production, gross primary production, and ecosystem respiration, respectively. Degrees of freedom (DF), sum of squares (Sum Sq), F- and P-values of the significance tests, and proportion of variance explained, as well as of the explained variance for main and interaction effects are given.

<table>
<thead>
<tr>
<th>Response Variable</th>
<th>Explanatory variable</th>
<th>DF</th>
<th>Sum Sq</th>
<th>% of variance explained</th>
<th>F-value</th>
<th>P-value</th>
<th>Sign.</th>
<th>% of the explained variance</th>
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1 Significance code (Sign.): 1 ≥ NS > 0.1 > * ≥ 0.05 > ** ≥ 0.01 > *** ≥ 0.001 > **** ≥ 0.0001.
Table S3.2 | Two-way ANOVAs on broad categories of ecosystem variables.

Results of three analyses of variance (ANOVA) performed on broad categories of ecosystem variables with climatic zone (C) and ecosystem type (E) as explanatory variables; model: $y \sim C + E + C:E$ (statistics for Figure 4b). Stocks (biomass, organic carbon, detritus), fluxes (gross primary production and ecosystem respiration), and turnover rates (decomposition rate) are pooled within each of these categories after the ecosystem variables (log values) are individually scaled. Degrees of freedom (DF), sum of squares (Sum Sq), F- and P- values of the significance tests, and proportion of variance explained, as well as of the explained variance for main and interaction effects are given.

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<th>DF</th>
<th>Sum Sq</th>
<th>% of variance explained</th>
<th>F-value</th>
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1 Significance code (Sign.): 1 ≥ NS > 0.1 > . ’ ≥ 0.05 > ‘*’ ≥ 0.01 > ‘**’ ≥ 0.001 > ‘***’ ≥ 0.001 > ‘****’ ≥ 0.
Table S3.3 | Non-parametric tests for climatic effect on ecosystem variables.

Results of Kruskal-Wallis tests on ranks (light headers) and groups given by multiple mean comparison post-hoc tests on rank sums (dark headers) performed on each individual ecosystem variable and on broader categories of ecosystem variables (i.e., stocks, fluxes and rates) testing the effect of climatic zone (C); model: \( y \sim C \). Stocks (biomass, organic carbon, detritus), fluxes (gross primary production and ecosystem respiration), and turnover rates (uptake and decomposition rates) were pooled within each of these categories after the ecosystem variables were individually scaled. See below the table for abbreviations. Degrees of freedom (DF), number of data points (n), Chi-squared and P-values of the Kruskal-Wallis tests are given. Significantly different groups have different letters.

<table>
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<tr>
<th>Ecosystem Variable</th>
<th>Kruskal-Wallis test on ranks</th>
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\(^1\) Significance code (Sign.): 1 ≥ NS > 0.1 > .’ > 0.05 > ‘*’ > 0.01 > ‘**’ > 0.001 > ‘***’ > 0.001 > ‘****’ ≥ 0.

Abbreviations: GPP = gross primary production; ER = ecosystem respiration; NEP = net ecosystem production; Decomp. Rate = decomposition rate; Temp = temperate; Trop = tropical.
Table S3.4 | Non-parametric tests for ecosystem type effects on ecosystem variables.

Results of Kruskal-Wallis tests on ranks (light headers) and groups given by post-hoc tests on rank sums for multiple mean comparison (dark headers) performed on each individual ecosystem variable and on broader categories (i.e., stocks, fluxes and turnover rates) testing the effect of ecosystem type (E); models: \( y \sim E \). Stocks (biomass, organic carbon, detritus), fluxes (gross primary production and ecosystem respiration), and turnover rates (decomposition rate) were pooled within each category after the ecosystem variables were individually scaled. Degrees of freedom (DF), number of data points (n), Chi-squared and P-values of the Kruskal-Wallis tests are given. Capital letters in dark headers are abbreviations for ecosystem types (see below the table). Significantly different groups have different letters.

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1 Significance code (Sign.): 1 ≥ NS > 0.1 > '.', 0.05 > *' ≥ 0.01 > '**' ≥ 0.001 > '***' ≥ 0.001 > '****' ≥ 0.

Abbreviations: GPP = gross primary production; ER = ecosystem respiration; NEP = net ecosystem production; Decomp. Rate = decomposition rate; F = forest; G = grassland; A = agroecosystem; D = desert; S = stream; L = lake; OP = ocean pelagic; OB = ocean benthic.
Table S3.5 | Non-parametric tests of mean differences among E x C combinations.

Results of Kruskal-Wallis tests on ranks (light row headers) and groups given by post-hoc tests on rank sums for multiple mean comparison (dark row headers) performed on each individual ecosystem variable testing the effect of ecosystem type (E) x climatic zone (C) combinations; models: y ~ EC. Number of data points (n), degrees of freedom (DF), Chi-squared and P- values of the Kruskal-Wallis tests are given. Significantly different groups have different letters. Note that for space reasons results are displayed in column (one Kruskal-Wallis test per column). Same tests but with clumped climatic variables, “Cold” and “Warm” for marine systems are shown in Table S3.12.

See below the table for abbreviations.

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1 Significance code (Sign.): 1 ≥ NS > 0.1 > .1 > .05 > .01 > .001 > .0001 > .00001 > 0.

Abbreviations: Eco = Ecosystem type; Clim = Climatic zone; F = forest; G = grassland; A = agro-ecosystem; D = desert; S = stream; L = lake; OB = ocean benthic; OP = ocean pelagic; Temp = temperate; Trop = tropical; Biom. = Biomass; Org. C = Organic carbon; GPP = gross primary production; ER = ecosystem respiration; NEP = net ecosystem production; Dec. = decomposition rate; Prod. = Productivity rate.
Table S3.6 | One-way ANOVAs on fluxes and rates of each ecosystem type.

Results of 18 analyses of variance (ANOVA) performed on gross primary production (GPP), ecosystem respiration (ER) and decomposition rate within each ecosystem type, with climatic zone (C) as explanatory variable; model: y ~ C (statistics for Figure 4c-e). Values were log-transformed and three zero values of GPP removed for that reason. Agro-ecosystem and desert ecosystems were removed because they are represented in only one climatic zone (temperate and arid, respectively). Degrees of freedom (DF), sum of squares (Sum Sq), F- and P-values of the significance tests, and proportion of variance explained are given.

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1 Significance code (Sign.): 1 ≥ NS > 0.1 > *' ≥ 0.05 > '***' ≥ 0.01 > '***' ≥ 0.001 > '***' ≥ 0.
Table S3.7 | Non-parametric tests on fluxes and rates of each ecosystem type.

Results of Kruskal-Wallis tests on ranks (light headers) and groups given by multiple mean comparison post-hoc tests on rank sums (dark headers) performed on gross primary production, ecosystem respiration, and decomposition rate within each ecosystem type testing the effect of climatic zone (C); model: $y \sim C$. Agroecosystem and desert ecosystems were removed because they are represented in only one climatic zone (temperate and arid, respectively). Degrees of freedom (DF), number of data points (n), Chi-squared and P-values of the Kruskal-Wallis tests are given. Significantly different groups have different letters.

<table>
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<th>Eco Var</th>
<th>Eco Type</th>
<th>n</th>
<th>Chi-squared</th>
<th>DF</th>
<th>P-value</th>
<th>Sign.</th>
<th>Multiple mean comparison post-hoc tests</th>
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<td>***</td>
<td>-            a      b    c    ab</td>
</tr>
<tr>
<td></td>
<td>Grassland</td>
<td>108</td>
<td>46.18</td>
<td>3</td>
<td>&lt;0.001</td>
<td>***</td>
<td>a                -      c    bc    b</td>
</tr>
<tr>
<td></td>
<td>Stream</td>
<td>210</td>
<td>9.51</td>
<td>4</td>
<td>0.05</td>
<td></td>
<td>a                a      a    a     -</td>
</tr>
<tr>
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<td>Lake</td>
<td>64</td>
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<td>2</td>
<td>&lt;0.001</td>
<td>***</td>
<td>a    b              b    -      -</td>
</tr>
<tr>
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<td>Oc. pelagic</td>
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<td>17.60</td>
<td>4</td>
<td>0.001</td>
<td>**</td>
<td>a    ab           b    ab   -    -</td>
</tr>
<tr>
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<td>Oc. benthic</td>
<td>65</td>
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<td>&lt;0.001</td>
<td>***</td>
<td>ab   a            a    a    b    a</td>
</tr>
<tr>
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<td>Forest</td>
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<td>***</td>
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</tr>
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<td>***</td>
<td>a    b            b    -      -    -</td>
</tr>
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<td>***</td>
<td>a    a            a    b    a    a</td>
</tr>
<tr>
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<td>Grassland</td>
<td>66</td>
<td>26.19</td>
<td>3</td>
<td>&lt;0.001</td>
<td>***</td>
<td>a    -            b    ab   b    ab</td>
</tr>
<tr>
<td></td>
<td>Stream</td>
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<td>&lt;0.001</td>
<td>***</td>
<td>a    ab           ab   c    bc   -</td>
</tr>
<tr>
<td></td>
<td>Lake</td>
<td>54</td>
<td>16.23</td>
<td>2</td>
<td>&lt;0.001</td>
<td>***</td>
<td>a    ab           b    b    -    -</td>
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<td>Oc. pelagic</td>
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<td>16.48</td>
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<td>&lt;0.001</td>
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<td>ab   -            b    b    a    a</td>
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<tr>
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<td>a    a            a    a    a    a</td>
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</table>

1 Significance code (Sign.): 1 ≥ NS > 0.1 > . > 0.05 > * > 0.01 > ** > 0.001 > *** > 0.

Abbreviations: Eco Var = ecosystem variable; Eco Type = ecosystem type; GPP = gross primary production; ER = ecosystem respiration; Dec. = decomposition rate; Oc. = Ocean; Arc. = arctic; Bor. = boreal; Temp. = temperate; Trop. = tropical.
Table S3.8 | Correlations between ecosystem variables and latitude.

Results of Pearson’s two-sided correlation tests between ecosystem variables within each ecosystem type and latitude (light headers) and slope and intercept of corresponding linear regression (dark headers) for significant correlations (P-value < 0.05) (statistics for Figs 7, S4.3, S4.4, and S4.5). Statistic t, degrees of freedom (DF), correlation coefficient (r), r squared, and P-values of the correlation tests are given.

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<th>Ecosystem Variable</th>
<th>Ecosystem type</th>
<th>t-stat.</th>
<th>Pearson’s two-sided correlation test</th>
<th>Linear regression</th>
<th>Sign.</th>
<th>Slope</th>
<th>Intercept</th>
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<td>r²</td>
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<td>0.118</td>
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<td>0.001</td>
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<td>***</td>
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<td>0.04</td>
<td>0.047</td>
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<tr>
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<td>0.01</td>
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<tr>
<td>(log values)</td>
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<td>-0.51</td>
<td>0.27</td>
<td>&lt;0.001</td>
<td>***</td>
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Supporting information: Multivariate ecosystem functioning  

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<th></th>
<th>Stream</th>
<th>Lake</th>
<th>Oc. pelagic</th>
<th>Oc. benthic</th>
<th>Dec. rate (log values)</th>
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<td>-2.39</td>
<td>-1.03</td>
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<td>-3.88</td>
<td>-2.39</td>
<td>-1.03</td>
<td>Grassland: -6.13 38 -0.70 0.50 &lt;0.001 *** -0.03 0.67</td>
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<td>-3.88</td>
<td>-2.38</td>
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<td>-1.03</td>
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<td>-2.82</td>
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1 Significance code (Sign.): 1 ≥ NS > 0.1 > ‘.’ ≥ 0.05 > ‘*’ ≥ 0.01 > ‘**’ ≥ 0.001 > ‘***’ ≥ 0.001 > ‘****’ ≥ 0.

Abbreviations: Org. C = organic carbon; NEP = net ecosystem production; GPP = gross primary production; ER = ecosystem respiration; Dec.= decomposition rate; Oc. = Ocean.
Table S3.9 | Non-parametric tests for climatic effect on NEP of each ecosystem type.

Results of Kruskal-Wallis tests on ranks (light headers) and groups given by multiple mean comparison post-hoc tests on rank sums (dark headers) performed on net primary production (NEP), within each ecosystem type testing the effect of climatic zone (C); model: $y \sim C$. Agro-ecosystem and desert ecosystems were removed because they are represented in only one climatic zone (temperate and arid, respectively). See below the table for abbreviations. Number of data points (n), degrees of freedom (DF), Chi-squared and P-values of the Kruskal-Wallis tests are given. Significantly different groups have different letters.

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<th>Ecosystem Type</th>
<th>Kruskal-Wallis test on ranks</th>
<th>Multiple mean comparison post-hoc tests</th>
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</tr>
<tr>
<td>Grassland</td>
<td>102</td>
<td>12.54</td>
</tr>
<tr>
<td>Stream</td>
<td>203</td>
<td>41.56</td>
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<td>58</td>
<td>1.29</td>
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$^1$ Significance code (Sign.): 1 $\geq$ NS $> 0.1 > \cdot > 0.05 > \cdot \cdot > 0.01 > \cdot \cdot \cdot > 0.001 > \cdot \cdot \cdot \cdot \geq 0.$

Abbreviations: Oc. = ocean; Arc. = arctic; Bor. = boreal; Temp. = temperate; Trop. = tropical; C = cold; w = warm.
Table S3.10 | Non-parametric tests for climatic effect within forests.

Results of Kruskal-Wallis tests on ranks (light headers) and groups given by multiple mean comparison post-hoc tests on rank sums (dark headers) performed on each ecosystem variable within forest ecosystems testing the effect of climatic zone (C); model: y ~ C (statistics for figure S4.5). See below the table for abbreviations. Number of data points (n), degrees of freedom (DF), Chi-squared and P-values of the Kruskal-Wallis tests are given. Significantly different groups have different letters.

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1 Significance code (Sign.): 1 ≥ NS > 0.1 > * ≥ 0.05 > ** ≥ 0.01 > *** ≥ 0.001 > **** ≥ 0.

Abbreviations: NEP = net ecosystem production; GPP = gross primary production; ER = ecosystem respiration; Bor. = boreal; Temp. = temperate; Trop. = tropical.
### Table S3.11 | Mean values, coefficients of variation and numbers of data points.

For each combination of ecosystem type, climatic zone and ecosystem variable, the mean value is in black, the coefficient of variation in grey and in brackets, the number of data points in red and in italics. See abbreviations below.

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<td>4.9</td>
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Abbreviations: Biom. = biomass; Org. C = organic carbon; NEP = net ecosystem production; GPP = gross primary production; Dec. = decomposition rate; Uptake = uptake rate.
Table S3.12 | Non-parametric tests of mean differences among E x C combinations.
Results of Kruskal-Wallis tests on ranks (light row headers) and groups given by post-hoc tests on
rank sums for multiple mean comparison (dark row headers) performed on each individual
ecosystem variable testing the effect of ecosystem type (E) x climatic zone (C) combinations;
models: $y \sim EC$. Degrees of freedom (DF), number of data points ($n$), Chi-squared and $P$-values
of the Kruskal-Wallis tests are given. Significantly different groups have different letters. Note that for
space reasons results are displayed in column (one Kruskal-Wallis test per column). These are same
the tests than in Table S3.6 but with clumped climatic variables, “Cold” and “Warm” for marine
systems. It gives the significantly different groups per ecosystem variable in Fig. 3 (boxplots). See
below the table for abbreviations.

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Significant groups are indicated by different letters. Abbreviations: Eco = Ecosystem type; Clim = Climatic zone; F = forest; G = grassland; A = agro-ecosystem; D = desert; S = stream; L = lake; OB = ocean benthic; OP = ocean pelagic; Temp = temperate; Trop = tropical; Biom. = Biomass; Org. C = Organic carbon; GPP = gross primary production; ER = ecosystem respiration; NEP = net ecosystem production; Dec. = decomposition rate; Prod. = Productivity rate.

Abbreviations: Eco = Ecosystem type; Clim = Climatic zone; F = forest; G = grassland; A = agro-ecosystem; D = desert; S = stream; L = lake; OB = ocean benthic; OP = ocean pelagic; Temp = temperate; Trop = tropical; Biom. = Biomass; Org. C = Organic carbon; GPP = gross primary production; ER = ecosystem respiration; NEP = net ecosystem production; Dec. = decomposition rate; Prod. = Productivity rate.

Significance code (Sign.): 1 $\geq$ NS $> 0.1 > \cdot \cdot > 0.05 > \cdot \cdot \cdot > 0.01 > \cdot \cdot \cdot \cdot > 0.001 > \cdot \cdot \cdot \cdot \cdot \cdot > 0.$
Table S3.13 | **Empirical relationships between pairs of ecosystem variables.**

Significant Pearson’s two-sided correlation tests between pairs of ecosystem variables across and within ecosystem types (light headers) in a log-log space (null values were removed from the analysis), and slope and intercept of corresponding linear regression (dark headers) (includes statistics for figures S4.6 and S4.7). Statistic t, degrees of freedom (DF), correlation coefficient (r), r squared and P-values of the correlation tests are given.

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Significance code (Sign.): 1 ≥ NS > 0.1 > * > 0.05 > ** > 0.01 > *** > 0.001 > **** ≥ 0.

Abbreviations: Org. C = organic carbon; GPP = gross primary production; ER = ecosystem respiration; Dec. = decomposition rate; Oc. = Ocean.
**Appendix S4 – Supplementary figures**

**Figure S4.1 | Relationships between ecosystem variables.**
Points and bars give median value and standard deviation respectively for the given ecosystem variables in each ecosystem type (colours) – climatic zone (shapes) combination. GPP and ER stand for gross primary production and ecosystem respiration, respectively, Black lines and grey areas give the median and the 95% confidence interval, respectively, of regressions realized in 10,000 iterations of bootstrapped values for each ecosystem x climatic zone combination (see methods). Text gives the median Pearson’s correlation coefficient for these 10,000 series of bootstrapped values and the percentage of significant correlations into brackets. Median and quantile regressions are not displayed when less than 75% of the correlations are significant.
Figure S4.2 | Principal Component Analysis (PCA) on median ecosystems.

Quantitative variables included in the analysis are median values of biomass, organic carbon, detritus, gross primary production (GPP), ecosystem respiration (ER), net ecosystem production (NEP), decomposition rate (Decompo. rate), and uptake rate for each combination of ecosystem type (colours in panel a) and climatic zone (shapes in panel a). Panels a and b represent the median ecosystems and the map of active variables, respectively, in the two first dimensions of the PCA with the percentage of explained variance into brackets in axes’ labels. In panel a, arrows highlight axes along which freshwater and terrestrial ecosystems are positioned according to changes in rates and fluxes from low to high, globally corresponding to colder or more arid to warmer climatic zones.
Figure S4.3 | Latitudinal trends in ecosystem stocks.

Solid circles show the data points. Colours denote ecosystem types. Lines show regression lines for significant correlations between latitude and stocks of **a** Biomass, **b** Organic carbon, or **c** Detritus, based on two-sided Pearson’s correlation tests. Pearson correlation coefficients and p-values are provided for these significant relationships (see legend for abbreviations of ecosystem types). Bottom parts of panels are zooming in finer scales than the one of top parts.
Supporting information: Multivariate ecosystem functioning

**Figure S4.4 | Latitudinal trends in mass-specific uptake rates.**

Solid circles show the data points. Colours denote ecosystem types. Lines show regression lines for significant correlations between latitude and uptake rates, based on two-sided Pearson’s correlation tests. Pearson correlation coefficients and p-values are provided for these significant relationships (see legend for abbreviations of ecosystem types).
Figure S4.5 | Latitudinal trends in GPP/ER ratios.

Solid circles show the data points. Colours denote ecosystem types. Lines show regression lines for significant correlations between latitude and uptake rates, based on two-sided Pearson’s correlation tests. Pearson correlation coefficients and p-values are provided for these significant relationships (see legend for abbreviations of ecosystem types). GPP and ER stand for gross primary production and ecosystem respiration, respectively.
Figure S4.6 | Functioning shift of forests among climatic zones.

Diagrams of ecosystem functioning in (a) boreal, (b) tropical and (c) arid forests. Squares represent stocks of biomass (B), detritus (D), and organic carbon (R). Straight arrows represent fluxes of gross primary production (GPP) and ecosystem respiration (ER), and bent arrows decomposition rates. Significant differences among panels for the different ecosystem variables are highlighted by differences in size of boxes or arrows. For instance, biomass is higher in tropical than in boreal or arid forests, and not different between boreal and arid forest (see statistical tests in Table S3.10). Dotted arrows represent fluxes for which we have not collected data.
Appendix S5 – Supplementary references


