



Toward a metabolic theory of catchments: Scaling of water and carbon fluxes with size

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Allometric scaling relations are widely used to link biological processes to body size in nature. Several studies have shown that such scaling laws hold also for natural ecosystems, including individual trees and forests, riverine metabolism, and river network organization. However, the derivation of scaling laws for catchment-scale water and carbon fluxes has not been achieved so far. Here, we focus on scaling relations of catchment green metabolism, defined as the set of ecohydrological and biogeochemical processes through which vegetation assemblages in catchments maintain their structure and react to the surrounding environment. By revising existing plant size–density relationships and integrating them across large-scale domains, we show that the ecohydrological fluxes occurring at the catchment scale are invariant with respect to the above-ground vegetation biomass per unit area of the basin, while they scale linearly with catchment size. We thus demonstrate that the sublinear scaling of plant metabolism results in an isometric scaling at catchment and regional scales. Deviations from such predictions are further shown to collapse onto a common distribution, thus incorporating natural fluctuations due to resource limitations into a generalized scaling theory. Results from scaling arguments are supported by hyperresolution ecohydrological simulations and remote sensing observations.

green metabolism | plant size–density relations | transpiration rate per unit area | resource limitation | ecohydrological fluxes

Since the pioneering works of Kleiber (1, 2), allometric scaling relations have been widely used to address biological processes (e.g., ref. 3). The usual form of these power laws is $B \propto M^b$ (1, 2, 4, 5), where B is the mean metabolic rate (arguably a field rate opposed to maximal or resting ones) and M is a species' mean mass (assumed to be properly defined). The allometric exponent b typically ranges between 2/3 and 3/4 (6–9) depending on embedding dimension D of the considered organism [say, its two- or three-dimensional structure because $b = D/(D + 1)$] (10). However, it is clear that proper insight into data analysis cannot ignore the fact that organismic masses and measured metabolic rates are actually correlated random variables, and thus scaling relationships need to be seen in the context of joint probability distributions. Scaling marginal distributions of organismic mass (11) and metabolic rates (12) and their interpretation in a proper probabilistic framework from experimental data or computations have been proposed (13). There exists a wealth of research evidence showing that such scaling arguments hold for organisms as well as for natural ecosystems. Laws linking river network organization (14–19), metabolic dynamics of individual plants (20–22), plant communities (23, 24) and forest ecosystems (25–28) are just some examples. Covariations in ecological scaling laws have also been examined in a framework on which we shall return in this paper (29).

Existing knowledge has mostly focused either on specific aspects [e.g., the river network and its metabolic functioning (30)] or on relatively small scales [e.g., from single organisms to plot scale plant assemblages (31)], while a comprehensive framework encompassing the heterogeneities observed at the scale of entire catchments is still missing to date. As topographically delineated water collectors, catchments represent a natural landscape unit (or control volume) whose boundaries are not arbitrarily delimited but rather defined by water flow through the land phase of the hydrologic cycle (32). By acknowledging the fundamental nature of the studies where the fluvial catchment acts as control volume rather than an arbitrarily defined spatial domain, we set the stage for integrating theories in ecology and hydrology. Spatially explicit process descriptions, supported by remote and field information, become feasible thus radically changing our capability to provide quantitative evaluations of ecosystem services. The metabolism of a catchment can therefore be broadly defined as “the set of processes through which the basin maintains its structure and responds to the environment” (33, 34). However,

Significance

Allometric scaling laws, positing that representative biological traits of an organism vary with body mass, describe the relation between a species' mean body mass to representative physiological rates, later extended to animals, plants, and entire ecosystems. One wonders whether similar relationships apply to the metabolism of a catchment, i.e. the set of processes through which it maintains its structure and responds to the environment. Of particular importance to that end are vegetation water and carbon fluxes, which we show to increase linearly with catchment size, yet displaying notable fluctuations ascribable to resource limitation. The combination of theoretical predictions and numerical simulations, supported by remote sensing and field observations, may lead to a theory linking metabolic fluxes to global carbon cycling.

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these processes occur at different spatiotemporal scales and include carbon and nutrient dynamics, vegetation processes, water and energy fluxes, as well as soil erosion and landscape evolution dynamics. As such, the catchment can be regarded as the stage where notions of biology, ecology, hydrology, and geomorphology intertwine. It is such complexity that has made the derivation of allometric scaling relations of catchment metabolism a daunting task.

A relevant step toward this direction was made by Rodríguez-Iturbe et al. (33), who first addressed the metabolic principles of river basin organization by envisioning nested subbasins as single organisms and addressing intraspecies scaling behavior. Notably, Rodríguez-Iturbe et al. (33) showed an allometric relation (with a power law exponent close to $2/3$) between the transpiration rate (intended by the authors as the catchment's "green" metabolism) and the total amount of runoff (surrogated by the nested sum of total contributing areas), which was here considered as a proxy of body mass of the basin as it approximates the water flow volumes. Such a result—which was derived following previous studies on hydrologic network allometry (35)—hinted to the idea that river basin metabolic activity is linked to the spatial organization of the underlying drainage network. However, in ref. 33, no clear distinction was made between terrestrial and riverine components of a catchment, for which the notions of body mass might be fundamentally different. Indeed, a central tenet of such work was the assumption that the adopted proxy for flow volume is representative of the catchment's body mass (36). Along these lines, recent studies showed that riverine biogeochemical functions (such as the uptake velocity of dissolved organic carbon in river networks) scale as power law functions of the drainage area (30, 37). In such contexts, the network structure clearly has an impact in affecting the amount of nutrients transported by a stream (38). Assuming flow volumes to be representative of the catchment mass is thus reasonable for riverine metabolic activity, the so-called "blue" metabolism (33), which involves distribution of resources via water transport [in analogy to blood vessels representing the network for the transport of metabolites (10, 36)]. However, the basic assumption that flow volume is a proxy of body mass (33) might need to be revised when focusing on the catchment terrestrial counterpart (particularly vegetation). Indeed, "green" metabolism is associated with processes of energy acquisition (photosynthesis) and energy utilization (respiration) carried out by the soil-plant system—clearly opposed to the river metabolic regimes, i.e., productivity and respiration in flowing waters (39). Rather than the drainage network itself, what drives the green metabolism is mainly related to the availability and distribution of resources (water and energy). Particularly, vegetation dynamics are driven by local soil moisture and temperature conditions which, despite being linked to topography (e.g., refs. 40 and 41), are not directly dependent upon the drainage network itself, especially in large catchments. A challenging open issue is therefore finding a common ground for combining green and blue metabolisms (limiting the scopes to landscape evolution in a stationary state) which are known to be often of comparable magnitude (39). In this context, an even more ambitious goal would be to further link green and blue metabolism to biodiversity patterns, and particularly to macroecological laws like observed species-area relationships, which were highlighted both in river systems (42) and for plants (43), and their covariations (29).

In this work, we explore the terrestrial dynamics typical of catchment metabolism with the analysis of vegetation water and carbon fluxes (we neglect here, as a first step, stores and fluxes related to belowground biogeochemical soil dynamics,

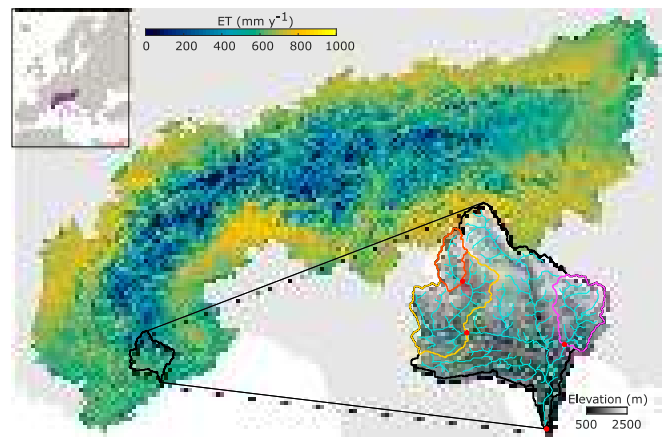


Fig. 1. Average yearly evapotranspiration (ET) flux over the European Alpine arch, as a result of the Tethys-Chloris model (readapted from ref. 44). The zoom highlights the Var and Tinee catchment, France. The main basin is featured with a black line, while three subcatchments are shown in red, yellow, and pink, as an example. Red dots refer to the outlet point of each basin.

biological diversity, and altogether blue metabolism). Specifically, we propose a framework by revising existing plant size–density relationships (31), which we integrate across large-scale catchment domains. Here, water and carbon fluxes deriving from assemblages of plant communities are used as proxies for the catchment metabolism, while the above-ground biomass (per unit area) acts as the specific mass of the terrestrial system. We show that green metabolic fluxes—e.g., transpiration rate and gross primary productivity—tend to an isometric scaling relation with respect to the basin size. Results from scaling arguments are verified through hyperresolution ecohydrological simulations across the European Alps (44), which represent an ideal case study owing to the wide range of elevation gradients affecting the availability of resources (Fig. 1) and therefore the catchment metabolic activity. Deviations from the predicted maximal scaling, resulting in suboptimal behavior of the system, are to be expected in heterogeneous organisms and are quantified here through marginal probability density functions.

From Single Plant to Catchment Metabolism: Theoretical Considerations

Enquist et al. (31) derived a mechanistic model for the relationships between density and mass in plant communities, by compiling literature data which included several species of herbaceous plants, shrubs, tree seedlings, mature evergreen, and deciduous trees. The starting point of their study was that whole-plant resource use (Q , metabolic rate) scales as the above-ground dry mass of the individual plant to the power of $3/4$. The resource use Q to which they refer is the whole-plant xylem transport, being a proxy for water and nutrient uses and photosynthesis, therefore for plant metabolism. Q has units of volume over time (i.e., $[L^3 T^{-1}]$, L and T being the length and time units, respectively).

Although the statistical validity of average biological quantities is debated (45), it can be assumed that the average rate of resource use per individual $\bar{Q}$ scales as the average plant mass ($\bar{M}$) as $\bar{Q} \propto \bar{M}^{3/4}$ in forest ecosystems and more in general in plant communities (27). Also, further assuming that i) plants compete for spatially limited resources, and ii) their growth is limited by the available resource supply, the relationship between the

maximal population density (number of individuals per unit area, $[L^{-2}]$) and the mass in ecological communities scales as $N_{\max} \propto \bar{M}^{-3/4}$. While we employ here maximum population density in line with previous works (31, 46), similar relationships are found for mean population densities against body mass (47, 48). As a result, the total rate of resource use per unit area $Q_{\text{tot}} [L T^{-1}]$ is invariant with respect to body size in plant communities, since the energy use per plant and plant density scale with reciprocal exponents, i.e., $Q_{\text{tot}} = N_{\max} \cdot \bar{Q} \propto \bar{M}^0$.

By definition, the product of population density by the average plant mass gives the above-ground biomass ($AGB [M L^{-2}]$) of the community per unit area (49), namely $AGB = N_{\max} \cdot \bar{M}$. Since the average above-ground mass scales with the population density as $\bar{M} \propto N_{\max}^{-4/3}$, it follows that $N_{\max} \propto AGB^{-3}$. By combining these relationships (details in [SI Appendix](#)), the rate of resource use (metabolic rate) per unit area results to be invariant with respect to the above-ground biomass per unit area, i.e.,

$$Q_{\text{tot}} \propto AGB^0. \quad [1]$$

Thus, not only Q_{tot} is independent of the community average plant mass [as shown by Enquist et al. (31)], but also of the AGB per unit surface area. Deviations from this behavior are ascribable to differences in the productivity of ecosystems (e.g., moving from a tundra to a forest) (50). One of the key peculiarities of terrestrial catchments is actually the heterogeneous and diverse vegetation characterizing them, with different parts reflecting different microclimatic conditions driving resource availability as well as land uses (44, 51, 52).

By envisioning the terrestrial part of catchments as an assemblage of plants, we hypothesize the extension of the above predictions to entire basins. Integrating Eq. 1 over a generic catchment with surface A gives

$$Q_A = \int_A Q_{\text{tot}} dA \propto \int_A AGB^0 dA \quad [2]$$

$Q_A [L^3 T^{-1}]$ being the cumulative resource use over the entire catchment surface, whereas Q_{tot} refers just to the unit element dA . Further observing that AGB^0 is a constant, Eq. 2 reduces to the linear relationship,

$$Q_A \propto A \quad [3]$$

implying that the metabolic rate of a large-scale vegetation community (here, a catchment) is isometric with respect to the size of the considered system.

Quantitative measures of terrestrial metabolism may include water fluxes such as transpiration (T) (33, 53) and evapotranspiration (ET) rates (31, 50), and carbon fluxes, namely net primary productivity (NPP) and gross primary productivity (GPP) (28, 54–56). The rate of resource use considered in this study is the transpiration rate T , being it intimately linked to the plant xylem transport (31, 57) and thus a quantitative measure of plant metabolism (31, 33). In natural environments, it is known that transpiration to evapotranspiration ratio is invariant on inter-annual timescales (e.g., ref. 58), with their ratio being remarkably constant across climates (59, 60). Therefore, being $ET \simeq T$ in terrestrial catchments (60), the two quantities are expected to follow the same scaling. In particular, under the assumption that $Q \sim T$, Eqs. 1 and 3 become $ET_{\text{tot}} \simeq T_{\text{tot}} [L^3 T^{-1} L^{-2}] \propto AGB^0$ and $ET_A \simeq T_A [L^3 T^{-1}] \propto A$, respectively. With regard to carbon fluxes, assuming ([SI Appendix](#)) that plant gross primary productivity scales linearly with transpiration (61–63), it follows that carbon-related fluxes (particularly NPP and GPP) should also scale linearly with A . This further translates in constant carbon use efficiency (CUE) and water use efficiency (WUE) with catchment size,

$$CUE_A = \frac{NPP_A}{GPP_A} \propto A^0, \quad WUE_A = \frac{GPP_A}{ET_A} \propto A^0. \quad [4]$$

Results

The total transpiration rate per unit area $T_{\text{tot}} (m^3 m^{-2} y^{-1})$ is shown in Fig. 2A, as a function of the specific above-ground biomass (i.e., per unit area). As predicted by scaling arguments (Eq. 1), the total resource use per surface area is invariant with respect to the mass per unit area ($T_{\text{tot}} \propto AGB^{0.001}$, with an uncertainty associated to the scaling exponent of ± 0.0002 and $R^2 = 0.006$). The integrated resource use T_A over the catchment area A (Fig. 2B) gives evidence of the predicted linearity (Eq. 3), with a power-law exponent equal to $0.988 (\pm 0.0004)$ and $R^2 = 0.999$. The SD overall follows the same trend, despite slight deflections (Fig. 2A and B), thus leading to an almost quadratic scaling of the variance with A , in line with ref. 11. The agreement with results from Rodriguez-Iturbe et al. (33) is shown in Fig. 2C,

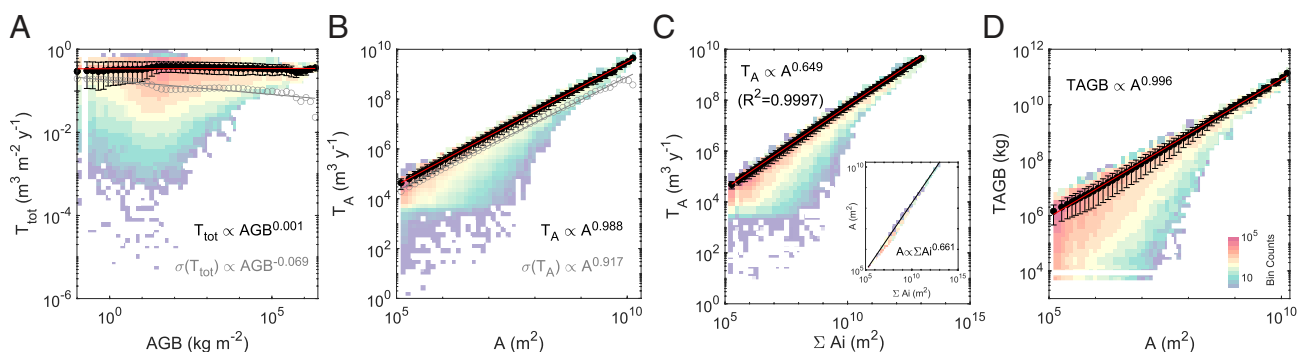


Fig. 2. (A) Log-log relationship between total transpiration rate per unit area T_{tot} and above-ground biomass per unit area AGB . (B) Transpiration integrated over the total catchment area $T_A = \sum_i T_{\text{tot},i} \cdot A_i$ as a function of A . See also [SI Appendix](#), Figs. S1 and S2 for ET , GPP , NPP , and CUE , WUE respectively. (C) T_A as a function of the sum of drainage areas, as shown in ref. 33. The *Inset* displays the relationship between catchment area and sum of drainage areas, characterized by a slope close to 2/3. (D) Total above-ground biomass $TAGB$ (kg) = $A \cdot AGB$ as a function of A . To increase readability, the data have been binned ([SI Appendix](#), Table S1) and shown with a logarithmic color scale. The colors code the number of observations in each bin (Bin Counts) and the red lines fit the binned data (black dots) according to the equations reported on the graphs ($R^2_{(A)} = 0.0060$, $R^2_{(B)} = 0.9998$, $R^2_{(C)} = 0.9997$, and $R^2_{(D)} = 0.9993$). Scaling of the SDs and corresponding regressions are reported in gray for (A and B) ($R^2_{\sigma(A)} = 0.7348$ and $R^2_{\sigma(B)} = 0.9964$).

where the same allometric exponent (close to two-thirds) clearly emerges with respect to the sum of drainage areas ($\sum A_i$), which is a consequence of a 2/3 power law scaling between A and $\sum A_i$ (35) (see *Inset* in Fig. 2C). Same outcomes are found for ET , GPP , and NPP , as shown in *SI Appendix, Fig. S1*. Predicted scalings are verified also for CUE and WUE (Eq. 4), which are invariant with respect to both the above-ground biomass per surface area and the catchment size (*SI Appendix, Fig. S2*). Results are further confirmed by FLUXCOM data (64) for GPP (*SI Appendix, Fig. S3*).

Albeit the density distribution highlights the greatest part of the data to be in line with predictions, deviations from the linear scaling clearly emerge (Fig. 2). Actually, the deterministic approach typical of scaling laws does not take into account the intrinsic and extrinsic fluctuations (e.g., due to thermodynamics, resource availability, etc.) which are indeed to be expected in living organisms as well as in natural ecosystems (65). It is as much as pretending that a population of organisms—be they animals or plants—is subsumed by the average mass or that the mean metabolic rate (e.g., in field conditions) recapitulates the maximal and basal ones. In the specific case analyzed here, such variations likely reflect the variability in resource availability (31) typical of highly heterogeneous alpine environments (e.g., refs. 66 and 67), together with any other anthropogenic or natural disturbances that may induce deviations from the emerging maximal behavior. It is interesting to note here that the observed sublinear deviations clearly emerge only when explicitly embedding the network structure within the sampling framework. As a matter of fact, when scaling properties are analyzed over square domains or noncontiguous points rather than catchments, the same scaling behavior is observed, but contributions to suboptimal deviations at small A values are minimal (*SI Appendix, Text and Fig. S4*), likely due to the random sampling of small areas across different topographic regions and vegetation covers.

While the maximum scaling to which the system tends to is captured by our arguments under the assumption of all resources being used (e.g., Eq. 3), fluctuations characterizing the suboptimal behavior can be described in light of the probability distributions of the catchment metabolic activity. Following the generalized scaling framework proposed by Zaoli et al. (13) (*Materials and Methods*), we revert our attention to the marginal distribution of green metabolism, namely the conditional probability density function $P(T_A|A)$ of the integrated transpiration rate T_A given the catchment area A (Fig. 3A). The density

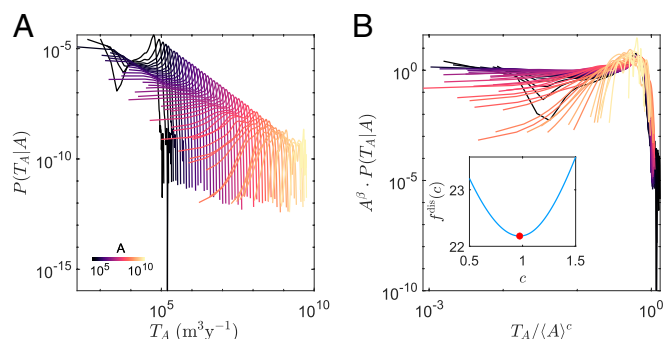


Fig. 3. (A) Bilogarithmic plot of the conditional probability of T_A (*Materials and Methods*). Each curve represents the data density function within the binned x-axis A of Fig. 2B. The color gradient ranges between $A = 10^5$ (darker) and $A = 10^{10}$ (lighter) m^2 . (B) Optimum collapse of the distributions in A by adopting the distance-based method (65) (*Materials and Methods*): The minimum of the $f^{dis}(c)$ function (red dot in the *Inset*) is found at $c = 0.9730 \pm 0.0120$.

functions highlight a wide range of possible shifts in the isometric scaling with respect to the predicted power-law exponent close to 1 resulting from average body mass and metabolic rate.

The conditional probabilities $P(T_A|A)$ tend to collapse onto a common universal distribution when appropriately rescaled (Fig. 3B) and expressed as a normalization term (A in this case) times a scaling function of $(T_A/\langle A \rangle^c)$ (13), with $\langle A \rangle$ the mean mass and c a scaling exponent (see Eq. 5 in *Materials and Methods*). By plotting $A \cdot P(T_A|A)$ against the above-defined scaling function it is possible to rescale the curves shown in Fig. 3A and make them collapse by varying the exponent c . Fig. 3B shows the best data collapse for different values of the body mass (A), with the optimal scaling exponent (evaluated following ref. 65; see *Materials and Methods*), being $c = 0.9730 \pm 0.0120$. The same is done for the resource per unit area (T_{tot}), with the optimal collapse found for $c = -0.004 \pm 0.0198$ (*SI Appendix, Fig. S5*). Note that in this case the conditional probability and the rescaled functions (*SI Appendix, Fig. S5 A and B*, respectively) barely differ from one another, being T_{tot} invariant with respect to AGB (*Materials and Methods*, Eq. 6). Density plots for ET , GPP , NPP , CUE , and WUE are displayed in *SI Appendix, Figs. S6–S8*.

To further investigate the origin of the observed deviations, we split the data on the basis of four elevation classes, ranging from the lowest to the highest elevations in the domain (Fig. 4A–D). Fig. 4E shows that the slope of the power-law deviates from 1 as a function of elevation. Particularly, we observe an increase in the allometric exponent b above $\sim 2,000$ m a.s.l., mirroring the increased scatter in the data. Again, the system clearly behaves following a distribution rather than being fully described by average values only, also with fluctuations varying as a function of elevation. We leave the mathematical framework embedding the elevation dependence in Eq. 5 for forthcoming work. Still, the variation in the coefficient values clearly indicates that high elevations impose a limit to metabolic activity. Data at hand allow us to observe that the variability is largely associated with a high percentage ($>80\%$) of bare rock, water body, glacier, or perpetual snow cover above certain elevations (*SI Appendix, Fig. S9A*). Together with the overall reduction of vegetated surface contributing to transpiration fluxes (and thus to green metabolic activity), it is also well known that plant productivity (GPP) decreases with elevation in temperature-limited systems (68). Furthermore, nutrient supply limitations, affecting photosynthetic activity, may derive from decreased nitrogen mineralization rates due to low temperatures (69) at high elevations, although these processes were not explicitly considered in the simulation results used here. We also observe catchments at lower elevations whose metabolic rate significantly deviates from the predicted linearity. This might be associated to managed areas, including croplands and built-up zones. They are characterized, on average, by 44% of grasslands and 53% of sparsely vegetated areas (*SI Appendix, Fig. S9 B and C*), marking again a reduction of surfaces that contribute to green metabolic fluxes.

Results obtained for GPP derived from FLUXCOM data (64) (*Materials and Methods*) for catchments in different climates are shown in Fig. 5. Despite the variability in the data, featured by the frequency distributions showed in Fig. 5A, the total GPP per unit area is found to be invariant with specific AGB for all the three domains, with an allometric exponent statistically indistinguishable from zero. Fig. 5B shows the linearity between GPP_A (resource use integrated over the area of the catchments) and A , with the allometric exponents significantly close to 1 across all climates. As expected, the different metabolic rate characterizing the three climates is evident in the (vertical) shift

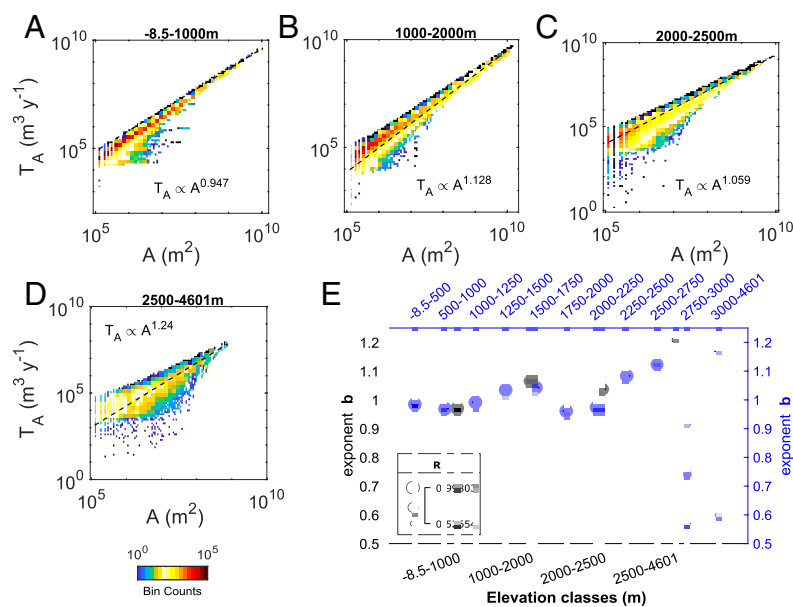


Fig. 4. Transpiration over the catchment area A as a function of 4 elevation classes (meters above the sea level), namely (A) -8.5 to $1,000$, (B) $1,000$ to $2,000$, (C) $2,000$ to $2,500$, and (D) $2,500$ to $4,601$ m a.s.l. (the legend reporting the number of observations in each bin applies for the four panels). (E) Values of the allometric exponent b ($T_A \propto A^b$) as a function of four (black axes) and eleven (blue axes) elevation classes. Error bars are linked to each bubble; the sizes of the circles indicate the goodness of the fitting (R^2).

of the three regression lines [with the tropical basin exhibiting the highest productivity (70)]. It is interesting to note that the Alpine catchment shows the highest deviation from the linear scaling among the three climates (see *Inset* in Fig. 5B). This reflects the strong elevation gradient characterizing this domain, which results in lower vegetation cover, temperature limitations, and, in turn, lower productivity, at high elevations. Some deviations with respect to the linear regression are found also in the Amazonian environment. However, in this case, neither the elevation gradient (*SI Appendix*, Fig. S10) nor a diversified land use characterization (more than 99.8% is evergreen broad-leaved forest, e.g., ref. 71) can justify the decreased productivity.

Marginal distributions with optimal data collapse are shown in *SI Appendix*, Fig. S11.

Discussion

By revising existing plant size–density relations and integrating them across large-scale domains, we showed that catchment metabolic activity (encoded here in the integrated water and carbon fluxes) tends to scale isometrically with the basin size. Particularly, the sublinear scaling observed for plant metabolism results in a linear scaling at catchment/regional scales. Sublinear intracatchment deviations were accounted by adopting marginal

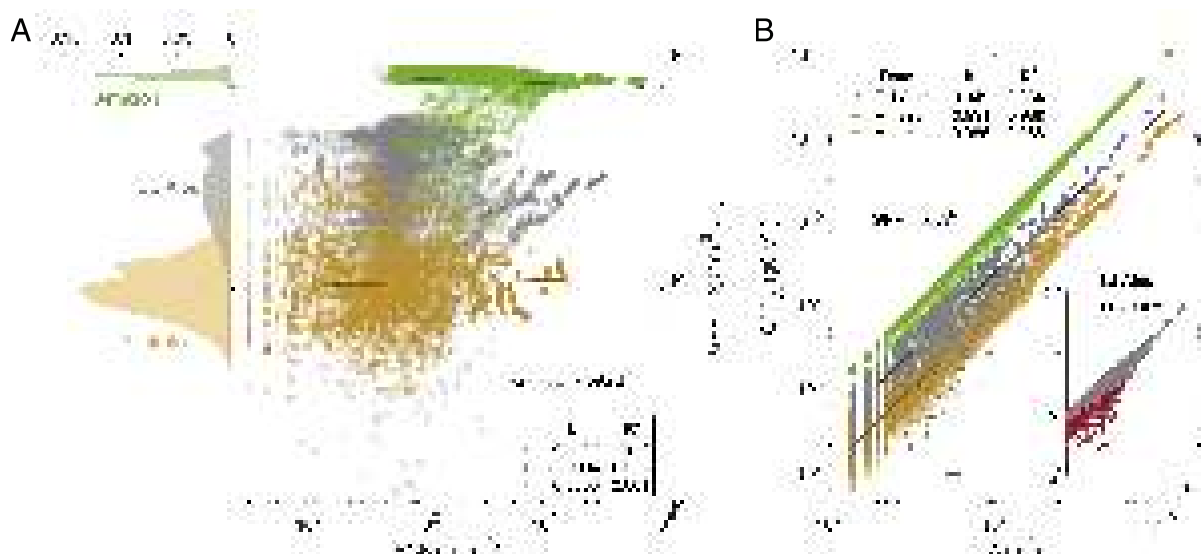


Fig. 5. (A) Annual Gross Primary Productivity (GPP) from FLUXCOM (64) as a function of the above-ground biomass for three catchments in the European Alps (gray), Amazon tropical forest (green), and South-East Australia (ochre). The frequency distribution of GPP of each dataset is shown to the *Left* of the scatterplot (values aligned with the y-axis). (B) GPP integrated over the catchment area A . The *Inset* highlights the points characterized by a mean elevation (H) above $2,500$ m (red dots). Legends report the allometric exponent b and R^2 of the fitted lines.

distribution functions and linked to resource limitations. Two theoretical aspects underpinning these results deserve further discussion. The first one deals with the assumptions of equal resource use and supply and their maximized utilization by plant populations (31), the second is related to the definition of the mass and metabolic rates of catchments.

To test the assumptions related to resource availability and use, we can recast the analysis in the framework of the Budyko curve (without making any assumption on the resource used by single plants and their density). Budyko's curve (72) relates water (e.g., precipitation P) and energy (e.g., potential evapotranspiration PET) availabilities to the long-term catchment evapotranspiration ET —one surrogate for the basin's green metabolism. Being the nonparametric Budyko expression for evapotranspiration $ET = P \cdot \sqrt{(1 - e^{-\phi}) \phi \tanh(\phi^{-1})}$ a function of the aridity index $\phi = PET/P$ only, one obtains $ET \propto P \cdot \sqrt{\phi}$. We observe that both P and PET scale linearly with the catchment size and, as a consequence, their ratio leads to an average invariant aridity index across the domain ($\phi \propto A^0$), which in turn leads to $ET \propto A$, further confirming the above-derived scaling (SI Appendix, Fig. S12). A more in-depth analysis seems to further suggest that the linearity holds better for arid catchments ($\phi \geq 1$) than for more humid ones (most likely colder in the Alps), characterized by $\phi < 1$ (SI Appendix, Fig. S12D).

Another key aspect of our derivation stems from the distinction between terrestrial (green) and riverine (blue) catchment metabolic activities, which leads to contrasting definitions of catchment mass as a function of drainage area. Previous work toward the definition of metabolic principles of river basin organization (33) assumed the sum of contributing areas as a surrogate for flow volumes and thus for the catchment mass—in analogy with the approximation of body mass with blood volumes proposed by ref. 36. Albeit plant transpiration was still accounted as a metabolic indicator, such assumption implicitly considered no distinction between riverine and terrestrial metabolism. This gave rise to the emergence of a two-thirds power law scaling between transpiration rate and sum of contributing areas. However, as shown by the scaling arguments here and their integration at the catchment scale, we argue that the catchment drainage area (which is proportional to the total above-ground biomass $TAGB$, Fig. 2D) is a more adequate estimate of the actual mass of the system when dealing with green metabolic activity, rather than the sum of nested contributing areas. The $2/3$ scaling postulated in ref. 33 is recovered when the nested sum of contributing areas is considered because of an existing power-law scaling between A and $\sum A_i$ (35). This suggests the need for a clear distinction between riverine and terrestrial catchment components when aiming at the definition of underlying metabolic principles.

While we focused here on what is generally termed green metabolism (encoded in vegetation water and carbon fluxes, or at least a significant part of it thereof), the search for a holistic definition of catchment metabolism needs to be further expanded to include other sources of metabolic activity, such as subsurface contributions to biogeochemical activities (where bacterial-generated fluxes may be relevant) and, as already mentioned, riverine metabolism due to in-stream processes. These processes are particularly relevant in relation to the key role of soils in the global carbon cycle (73) and the increasingly recognized role of inland waters in processing considerable amounts of organic carbon in their networks (74, 75).

It is clear that deriving a comprehensive metabolic theory of catchments is a challenging task. So far, notable efforts have demonstrated that metabolic fluxes typical of catchments can be actually described through scaling laws. For example, dissolved

organic carbon in rivers scales allometrically with the catchment size (30), while other biogeochemical riverine fluxes reach a superlinear behavior (37). From the work here it emerges that (areal) terrestrial fluxes asymptotically tend to an isometric scaling with the basin size, as regulated by the allometric scaling of plant metabolism and population density (31), while sublinear deviations emerge due to natural fluctuations of the system and resource limitations.

Whereas observed sublinear deviations are largely ascribable to a reduction in vegetation cover at high elevation, biological rates are also largely affected by the physical constraint of temperature, whose effect on soil-vegetation dynamics and carbon cycling is well established from a metabolic perspective (5, 76–81). Further contributions to natural deviations in terrestrial systems can be attributed to the coexistence of plant species with different adaptation strategies and traits (55, 82, 83), although this aspect alone seems unlikely to explain the entirety of the observed scatter (84). Last, a unified picture encompassing all the above interactions shall not neglect the relevance of biological diversity, which has been historically and largely addressed through species-area relationships (e.g., ref. 85).

Despite the common setting represented by catchments—where both riverine and terrestrial features occur and contribute to the identification of the basin itself—such theories still appear largely decoupled from one another. A critical aspect lies in the fact that terrestrial fluxes are essentially areal variables (in two dimensions), while for riverine transport and related biogeochemical processes, one should account for three-dimensional flowing volumes. Further research is therefore needed to unravel the possibility of merging the green and blue metabolism within a unified theoretical framework.

Materials and Methods

Verification Against Numerical and Remote Sensing Data. We verify the above scalings across different domains and climates, through i) high-resolution numerical experiments for the European Alps and ii) remote sensing data for tropical, alpine, and semiarid catchments.

Regarding the former, we used the distributed outcomes of water and carbon fluxes obtained by Mastrotheodoros et al. (44) with the mechanistic ecohydrological Tethys-Chloris (T&C) model (86). By accounting for the principal components of the hydrological cycle and vegetation dynamics, T&C computes the water, energy, carbon, and nutrient balances at the land surface and explicitly accounts for lateral water transfer and topographic effects on radiation. As proxies for Q we used T , ET , GPP , and NPP averaged over a period of three hydrological years (2001 to 2003) and obtained for every grid point i of the domain (Fig. 1), at $\Delta x = 250$ m resolution (for details, see ref. 44). In our analysis, every square cell of the Digital Elevation Model (DEM) is taken as outlet point (total 4.12 million points) for the derivation of nested subcatchments. It results that the minimum possible catchment is defined by one pixel, with area Δx^2 . The extraction of drainage networks was implemented following typical D8 algorithms (87, 88). At any location of the domain the rate of resource use per unit area Q_{tot} is computed as the sum over the number of cells pertaining to every catchment (i.e., each upstream site draining into it) and divided by the considered basin area $A = \sum_i \Delta x_i^2$: $Q_{\text{tot}} = \sum_i Q_i \cdot \Delta x_i^2 / A$. Above-ground biomass per unit area AGB_i was taken from the global dataset provided by ref. 89 for the year 2010 and resampled at our target resolution (Δx). At any location i , $AGB = \sum_i AGB_i$. To avoid uncertainties related to the exact values of AGB at the level of one or a few hectares (90), we show results for catchments consisting of at least two pixels, whose area is of the order of 10^5 m². This choice does not affect the resulting scalings.

We further used machine learning-based global estimates of GPP (applied to flux-tower observations) provided by FLUXCOM (64) to verify results from scaling arguments and numerical simulations. Specifically, we evaluated results across the entire European Alps and further compared one alpine large-scale

catchment (Adige river basin, approx. 12,200 km², outlet point coordinates: 45.14 lat, 11.24 lon) with other two basins characterized by similar sizes but different climates. Particularly, we considered a catchment of approx. 30,000 km² located in the tropical rainforest of the Amazon basin (Rio Içana basin, outlet point coordinates: 0.70 lat, -67.41 lon) and one in the arid steppe of South-East Australia (Murrumbidgee river basin, approx. 22,200 km², outlet point coordinates: -34.21 lat, 144.57 lon). The three catchments were selected on the basis of the available eddy covariance flux towers located nearby (*SI Appendix, Fig. S13*), in order to limit uncertainties in FLUXCOM estimates (64). For the three basins, all the nested subcatchments were extracted by taking again every cell of the DEM (derived from ref. 91) as outlet points, and annual GPP and AGB were then evaluated over the area of interest.

Marginal Distributions. Following previous works (13, 65), we express the marginal probability density function of the metabolic rates (i.e., the generic resource use integrated over the catchment surface $Q_A \propto A$) as

$$P(Q_A|A) = A^{-\beta} f\left(\frac{Q_A}{A}\right), \quad [5]$$

where the leading term is for normalization ($\beta = 1$, following the framework derived in ref. 13), $f(x)$ is a general scaling function constrained by the limits $f(x) \rightarrow 0$ for $x \rightarrow \infty$ and $f(x)$ tends to a constant for $x \rightarrow 0$, and c is the scaling exponent of the Kleiber's law (1) for mean mass (A). Note that a similar formulation for Eq. 5 was already proposed by ref. 6. Distributions are evaluated for binned data along the A -axis (*SI Appendix*). When considering the total resource use per unit area, being $Q_{\text{tot}} \propto \text{AGB}^0$, Eq. 5 becomes

$$P(Q_{\text{tot}}|\text{AGB}) = (\text{AGB}^0)^{-\beta} f\left(\frac{Q_{\text{tot}}}{(\text{AGB})^c}\right). \quad [6]$$

After rescaling with respect to the term $\langle A \rangle^c$ (Eq. 5) and $\langle \text{AGB} \rangle^c$ (Eq. 6), i.e., the mean value of each bin, the best collapse of the distributions is obtained through the distance-based method developed by Botte et al. (65). The method computes the function $f^{\text{dis}}(c)$, i.e., the overall sum of the Euclidean distances between points of each rescaled distribution pair, for values of the scaling exponent $c = 1 \pm 0.5$ (Eq. 5) and $c = 0 \pm 0.5$ (Eq. 6), equally spaced every 0.001 step. Thus, the minimum value of $f^{\text{dis}}(c)$ represents the best distributions collapse.

Data, Materials, and Software Availability. Previously published data were used for this work (<https://doi.org/10.1038/s41558-019-0676-5>) (44).

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