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Terrestrial ecosystems buffer inputs through storage and recycling of elements

Marie Spohn · **Felipe Aburto** · **Todd A. Ehlers** · **Nina Farwig** ·
Patrick J. Frings · **Henrik Hartmann** · **Thomas Hoffmann** ·
Annegret Larsen · **Yvonne Oelmann**

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Abstract This study presents a conceptual framework of buffering through storage and recycling of elements in terrestrial ecosystems and reviews the current knowledge about storage and recycling of elements in plants and ecosystems. Terrestrial ecosystems, defined here as plant-soil systems, buffer inputs from the atmosphere and bedrock through storage and recycling of elements, i.e., they dampen and delay their responses to inputs. Our framework challenges conventional paradigms of ecosystem resistance derived from plant community dynamics, and instead shows that element pools and fluxes have an overriding effect on the sensitivity of ecosystems to environmental change. While storage pools allow ecosystems to buffer variability in inputs over short to intermediate periods, recycling of elements enables ecosystems to buffer inputs over longer periods. The conceptual framework presented here improves our ability to predict the responses of ecosystems to environmental change. This is urgently needed to define thresholds which must not be exceeded to guarantee ecosystem functioning. This study provides

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M. Spohn (✉)
Biogeochemistry of Forest Soils, Department of Soil and Environment, Sveriges Lantbruksuniversitet (SLU), Lennart Hjelms väg 9, Uppsala, Sweden
e-mail: marie.spohn@slu.se

F. Aburto
Laboratorio de Investigación en Suelos, Aguas y Bosques (LISAB), Facultad de Ciencias, Forestales Universidad de Concepción, Victoria 631, Concepción, Chile
e-mail: feaburto@udec.cl

T. A. Ehlers
Department of Geosciences, University of Tübingen, 72076 Tübingen, Germany
e-mail: todd.ehlers@uni-tuebingen.de

N. Farwig
Conservation Ecology, Department of Biology, University of Marburg, Karl-von-Frisch-Str. 8, 35043 Marburg, Germany
e-mail: farwig@uni-marburg.de

P. J. Frings
Earth Surface Geochemistry, Section 3.3, GFZ German Research Centre for Geosciences, Telegrafenberg, 14473 Potsdam, Germany
e-mail: patrick.frings@gfz-potsdam.de

H. Hartmann
Department of Biogeochemical Processes, Max Planck Institute for Biogeochemistry, Hans-Knoll Str. 10, 07745 Jena, Germany
e-mail: hhart@bgc-jena.mpg.de

T. Hoffmann
Department of Hydromorphology, Sediment dynamics and - management, Federal Institute of Hydrology, Am Mainzer Tor 1, 56068 Koblenz, Germany
e-mail: thomas.hoffmann@bafg.de

a framework for future research to explore the extent to which ecosystems buffer variability in inputs.

Keywords Element storage · Nutrient recycling · Soil element cycling · Buffer · Storage mobilization

Introduction

Terrestrial ecosystems, by nature of their location at or near Earth's surface, are sensitive to the input and output of elements by different atmospheric, geologic, geomorphic, hydrologic, and ecologic processes. Climatic processes active 'above' an ecosystem influence the fluxes of nutrients and water into and out of an ecosystem. Furthermore, the composition and properties of bedrock underlying an ecosystem set the template for nutrient and element availability as inputs to the system from 'below' as well as outputs from the system by solute transport (Fig. 1). However, ecosystems have the ability to reduce their reliance on external inputs of elements and water, and thereby decrease their sensitivity to variations in the rate of inputs through storage and recycling. This property has been termed resistance by some authors (Pimm 1984; Connell and Ghedini 2015; Nimmo et al. 2015), even though it has proven difficult to explain the factors that produce ecosystem resistance (Connell and Ghedini 2015; Nimmo et al. 2015; Willis et al. 2018). In this review, we focus on developing the concept of buffering in ecosystems to provide a process-based understanding of the extent to which ecosystems can minimize their sensitivity to changes in the fluxes of inputs through storage and recycling.

Recently, Timpane-Padgham et al. (2017) performed a meta-analysis to identify ecosystem attributes that confer resistance or resilience to climate change. Of the 170 publications they analyzed, none identified ecosystem nutrient storage or recycling as a factor associated with resistance or resilience. Instead, the focus falls on species- to ecosystem-level ecological attributes (growth rates, diversity, species interactions, etc.). In this contribution, we develop the concept of ecosystem buffers as a mechanistic, processed-based approach to understand the ability of ecosystems to resist changes in their environment. This framework makes the testable prediction that ecosystems with large internal storage pools (relative to their supply rate) and effective recycling of nutrients buffer external inputs more effectively than ecosystems with small pools and small rates of nutrient recycling. The buffering framework attributes ecosystem responses to inputs to tangible pools and fluxes, whereas the concept of resistance fails to facilitate a mechanistic, process-based understanding of ecosystem functioning, and thus has difficulties to predict resistance or even to explain what causes resistance in ecosystems (Nimmo et al. 2015; Willis et al. 2018). The framework suggested here provides a quantifiable metric useful in diverse arenas such as long-term geochemical budgeting (e.g. Uhlig and von Blanckenburg 2019), development of ecosystem conservation and restoration strategies, identification and prediction of potential tipping points, and as explanatory variables in resilience analyses (e.g. Seddon et al. 2016; Willis et al. 2018). A quantifiable metric of the buffer capacity of ecosystems is essential for identifying the planetary boundaries that define a safe operating space for humanity on planet Earth (Steffen et al. 2015).

Compared to geological time scales, the period of time over which terrestrial ecosystems buffer variability in inputs are small, and depend on the turnover time of the buffer pool. However, compared to the lifespan of many animal species, these time periods are long. Thus, buffering of external inputs allows ecosystems to maintain their structure and functioning for periods of time during which many generations of one species (e.g. animals and shot-lived plants) develop. Buffering of inputs in ecosystems prevents small to intermediate changes in external factors leading to quick shifts in the ecosystem structure and functioning.

Storage and recycling of elements in ecosystems have been studied in biogeochemistry and ecosystem ecology for many years (e.g., Jordan et al. 1972; Vitousek and Reiners 1975). In addition, the question

A. Larsen
Soil Geography and Landscape, Wageningen University and Research, Droevendaalsesteeg 3,
6708PB Wageningen, The Netherlands
e-mail: anngret.larsen@wur.nl

Y. Oelmann
Geoecology, Department of Geosciences, University of Tübingen, Rümelinstr. 19-23, 72070 Tübingen, Germany
e-mail: yvonne.oelmann@uni-tuebingen.de

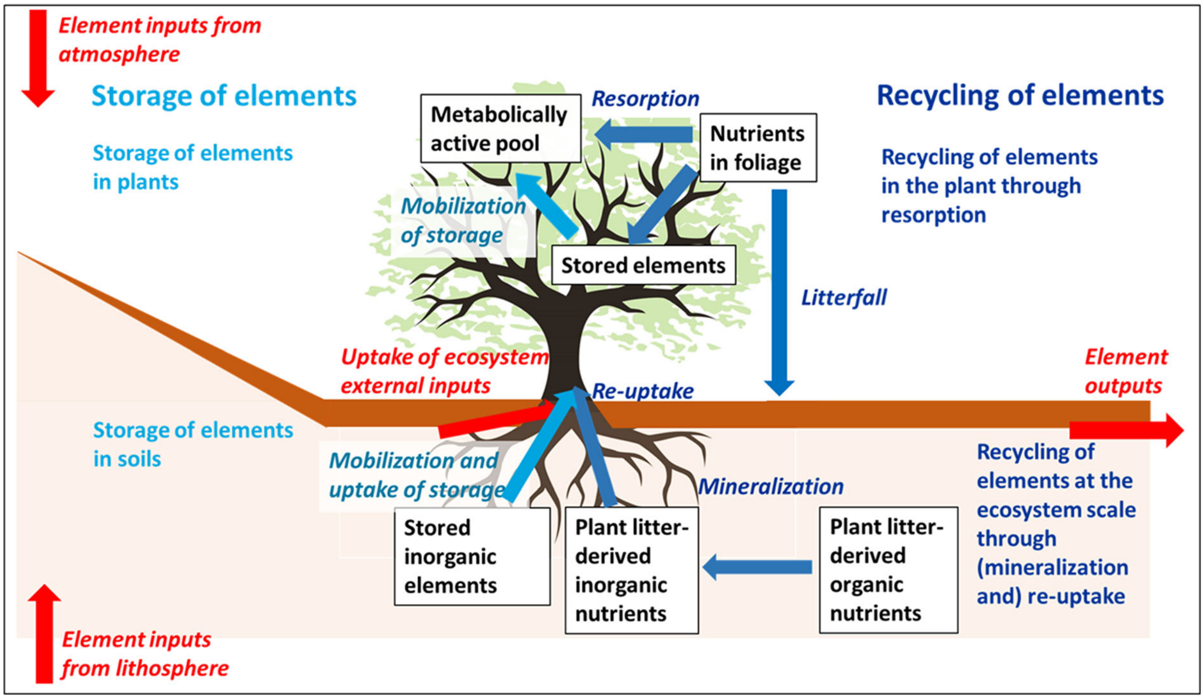


Fig. 1 Storage of elements as well as processes of nutrient recycling decrease the sensitivity of ecosystems to external inputs. Pools are shown by white boxes with black frames. Fluxes of external inputs to the ecosystem are indicated by red arrows, and ecosystem internal fluxes are indicated by blue arrows. Fluxes of nutrient recycling are indicated by dark blue arrows, and fluxes of elements out of storage pools are indicated by light blue arrows (colour figure online)

of how recycling of nutrients affects ecosystem stability has been intensively discussed in ecosystem ecology, particularly in the in the 1970s and 1980s (e.g. May 1972; De Angelis 1980). Here, we build on this basis and extend the knowledge of storage and recycling of elements by reviewing recent advances and providing a unifying framework of buffering in terrestrial ecosystems via storage and recycling.

This review complements the advances of the previous work by: (1) proposing a unifying concept of buffers in ecosystem based on a review of existing concepts, and (2) summarizing current knowledge about storage and recycling of elements in ecosystems. We concentrate on storage and cycling of the macronutrients N, P and K as well as C while acknowledging the role of other elements when appropriate.

Conceptual framework

Review of concepts of buffering

The concept of a buffer is found in many environmental science disciplines, including soil science, biogeochemistry, hydrology, geomorphology, plant ecophysiology, and ecology. These disciplines have developed subtly different concepts of what a buffer is and how it functions. Here we summarize the various concepts of buffers across these disciplines, identify the commonalities, and develop a quantitative framework to define the buffer capacity of an ecosystem. Based on this, we present a quantitative framework for the buffering capacity of an ecosystem with respect to a given element or compound.

In soil science and biogeochemistry, the concept of a buffer is frequently used in the context of anthropogenic inputs to ecosystems. For example, in soil science, the term often refers to the capacity of soils to neutralize proton inputs due to the presence of carbonates, silicates and organic matter (OM) that react with protons at specific rates. Thus, the buffer capacity of a soil is defined as the maximum flux of protons entering the soil that does not induce a change in soil pH (Ulrich 1983; Chadwick and Chorover 2001). In biogeochemistry, the term buffer has been used, for example, with respect to anthropogenic P inputs to catchments. These inputs can bind to soil/sediment up to a limit, after which they enter the fluvial system when the buffer capacity of the soil/sediment is exceeded and no more P-binding sites are available (Jørgensen and Mejer 1977; Doody et al. 2016; Schippers et al. 2006; Kusmer et al. 2019). In this case, buffering results from the ability of the system to internally store P. Previous work defines the buffer capacity as the reciprocal of the change in an ecosystem state variable (e.g. P concentration of a water body) per unit of forcing applied (e.g. per unit P input) (Jørgensen and Mejer 1977). More recently, buffer capacity was defined as one minus the ratio of P outputs to P inputs in a watershed (Kusmer et al. 2019). In all of these examples, a buffer is a pool of a reactant, and buffer capacity is defined as the size of the available pool of the reactant (i.e. quantity of available reactants or binding sites). In these examples, a buffered system is one in which an input of a substance (e.g. protons, P, etc.) induces a proportionally smaller change in the system functioning because the pool of reactant is sufficient to immobilize, neutralize, or otherwise retain the input.

In hydrology, the term buffering describes the properties of water reservoirs that alleviate asynchronicities between water supply and demand and mitigate the effects of high rainfall variability on water availability (e.g., Riebsame 1988; Calow et al. 2010; Pritchard 2017). In geomorphology, the term buffering is used with respect to the delayed and dampened sediment output from a catchment that results from internal storage of sediment (Brunsden and Thornes 1979; Armitage et al. 2013; Hoffmann 2015). The term buffer often also refers to landforms that act as barriers and disrupt the sediment transport pathway (Harvey 2002; Fryirs et al. 2007), or to thresholds that need to be exceeded before sediment transport is initiated (Schumm 1973). Thus, in both hydrology and in geomorphology, buffering results from the storage of matter (water or sediment).

In plant ecophysiology, buffering refers to an alleviation of the effect of temporarily low nutrient or water availability on biomass production by storage of resources within plants (Millard and Grelet 2010). Thus, as above, buffering is caused by the storage of mass. Here, the quantification of buffering is achieved not by comparing the input of a certain substance to the output of the same substance (cf. P, water, sediment), but rather by comparing the input (water or element uptake) to biomass production as the response signal. The term buffering has also been used in ecology to describe a reduction in the temporal variance of productivity of an ecosystem in a fluctuating environment in response to an increase in biodiversity, albeit without a clear definition of the processes causing the buffered response (Yachi and Loreau 1999; Isbell et al. 2015). The concept of buffers is also popular in conservation ecology, where it refers to a protective zone of land around a sensitive area that lessens the impact of human disturbances (Sliva and Dudley Williams 2001).

Buffering of inputs in ecosystems: quantitative framework

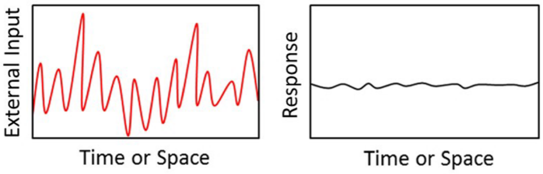
To facilitate a more mechanistic understanding of buffers in plant-soil systems we develop an approach using mass-balance models that encapsulate the buffering of variable inputs. Our approach merges most concepts reported in "Review of concepts of buffering" section. Three concepts form the basis for our approach (Box 1 part A). First, *buffering* is a system behavior that consists of dampening and/or delaying the response of a state variable to an external, varying input. Second, a *buffer* is an ecosystem pool. Third, *buffer capacity* is the ability of a system to buffer external inputs, which reduces the sensitivity of the system to external inputs, and depends on the size and turnover of the buffer pool.

While the term buffering has mostly been used with respect to temporal changes in inputs, we propose to widen this concept and include spatial changes in inputs (see Box 1 part A). This makes the concept more useful to ecology and environmental science, which usually have data with high spatial resolution but limited temporal resolution (see also "Buffering of variable inputs through storage and recycling of elements" section).

In the following part of this section, we build upon the previous general concepts and show how a simple mass-balance model can describe buffering of temporally varying inputs. We focus on a simplified approach here for a single buffer pool and a linear

(a) Buffering

Buffering: System behavior that dampens and/or delays the response to an external input.



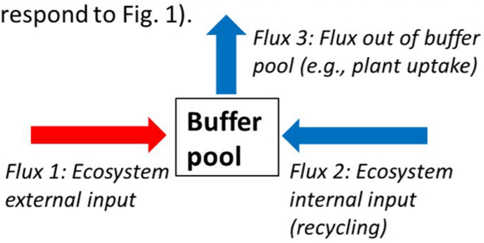
Buffer capacity: Ability of a system to buffer external inputs, reduces the sensitivity of an ecosystem to external inputs, and depends on the size and turnover of the buffer pool

Buffer pool [kg m^{-2}]: System component (pool) involved in buffering

Threshold/Tipping point: Critical point in the system state at which the system changes fundamentally, can occur if buffer capacity is exceeded

(b) Buffering and recycling

The buffer pool can be refilled by ecosystem internal fluxes (recycling) which can compensate for low external inputs. (The arrows and their colors correspond to Fig. 1).



Red arrow: flux of external inputs to the buffer pool

Blue arrows: fluxes of internal nutrient cycling in the ecosystem

Box 1 Definitions. Please notice that the colors in part A correspond to the colors in Figs. 2, 3, 4 and 5 and that the colors of the arrows in part B correspond to the ones in Fig. 1

dependence of the output fluxes on the pool size. This approach over-simplifies ecological complexity, but suffices as a way of conveying the concepts of a buffer and buffer capacity.

The rate of change of the pool size (Box 1) is given by the difference between the input and the output fluxes to the pool:

$$\frac{dM}{dt} = Q_{in} - Q_{out} \tag{1}$$

where $M(t)$ is the pool size [mass] of some substance at time t and Q_{in} and Q_{out} are the sum of all fluxes of that substance into and out of the pool [mass time^{-1}], respectively. For many systems, Q_{out} can be approximated as a linear function of M :

$$Q_{out} = kM \tag{2}$$

where k is a rate constant, with units of time^{-1}. For a system at steady state, the size of the pool M is constant ($\frac{dM}{dt} = 0$, and thus $Q_{in} = Q_{out}$) and the turnover time (τ, units of time) of the pool is defined as the ratio of the pool size (M) to the input flux Q_{in}, or as the inverse of k:

$$\tau \equiv \frac{M}{Q_{in}} = \frac{1}{k} \tag{3}$$

Variations in inputs to a system are often cyclical or quasi-cyclical (the functional form of the cyclicity is process dependent). For the sake of simplicity, we consider that Q_{in} varies sinusoidally with time, a reasonable approximation of many periodic environmental changes:

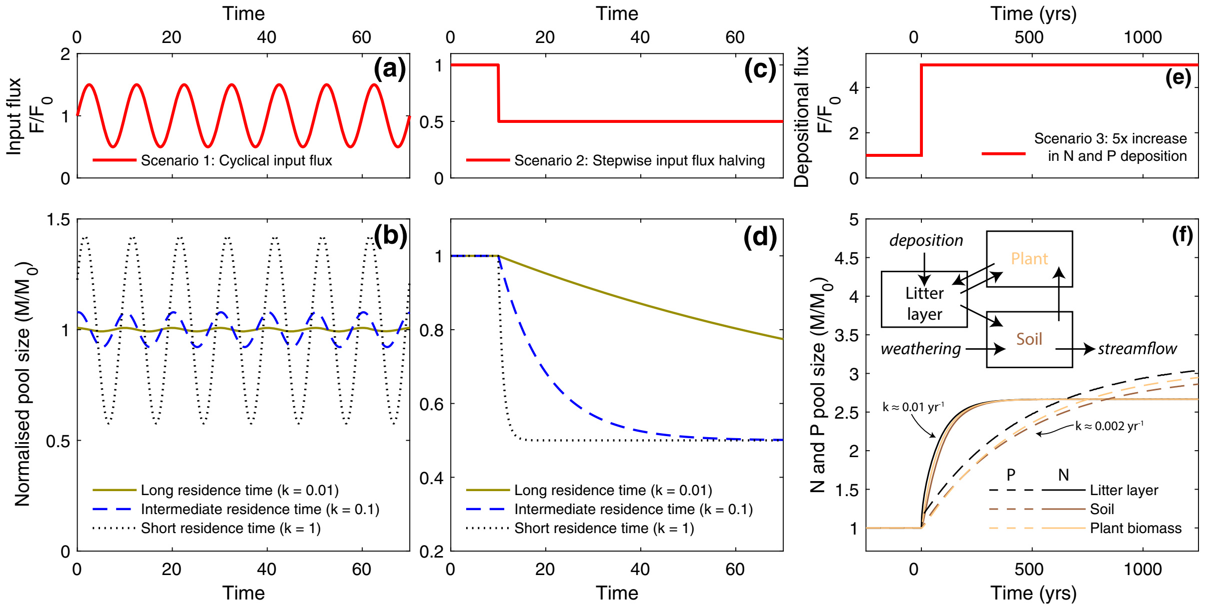


Fig. 2 The response of well-buffered and poorly-buffered pools and systems of pools. Panels **A**, **C**, and **E** show the input flux over time and panels **B**, **D**, and **F** show the normalized pool size. *Scenario 1* (Panels **A**, **B**) considers cyclical change in input fluxes, varying sinusoidally by ± 50% around a mean. The response of an ecosystem pool (**B**) depending on the period of oscillation of the input flux relative to the turnover time of the pool (see main text for details). Time on the x-axis is given in units of multiples of the turnover time of the pool. Both x- and y-axes are non-dimensional. *Scenario 2* (Panels **C**, **D**) considers a stepwise halving of an input flux, where well-buffered pools (with long turnover times) respond with a larger delay than poorly-buffered pools. *Scenario 3* (Panels **E**, **F**) demonstrates that the concept is extendable to multi-pool systems. A ×5 increase in N and P deposition rates (panel **E**) to an Eucalyptus forest is prescribed (data from Attiwill and Adams (1993) as reported in Spohn and Sierra (2018)). The resulting changes in the sizes of the three pools are derived by solving a system of ordinary differential equations (see text for details). In this example, the relative change in the P pools at a given time is smaller than the N pools, indicating the P cycle is more strongly buffered

$$Q_{(t)} = a + b \times sin(\omega t) \tag{4}$$

where a is the mean of Q_{in} and b is the amplitude of oscillation in Q_{in}. The frequency of oscillation ω equals 2π/T, with T being the period of oscillation (in the same units as t). This cyclicity may represent any timescale, including (sub-)annual (e.g. diurnal to seasonal), multiannual, (e.g. El Niño-Southern Oscillation) to centennial or longer (e.g. solar insolation or Milankovitch cycles). Substituting Eqs. 2 and 4 into Eq. 1 permits an analytical solution for temporal changes in the pool size M (Kercher 1983; Sarmiento and Gruber 2006):

$$M(t) = a/k + \frac{b}{\sqrt{\omega^2 + k^2}} \cdot sin(\omega t + \phi) \tag{5}$$

where a is the mean of Q_{in} and b is the amplitude of oscillation in Q_{in}.

In this formulation, ϕ captures the phase shift of the pool size relative to the cyclicity of Q_{in}, the value of which is given by tan$\varphi = \omega/k$. Thus, the relationship between the frequency of oscillation of the input flux (ω) and k determines the phase shift of the oscillation of M. Equation 5 also shows that (1) the mean pool size is directly proportional to the mean input (a/k), and that (2) the amplitude of the variation of the pool size is related to the amplitude of the variation in inputs and the relative timescales of input oscillation w and pool response k ($\frac{b}{\sqrt{\omega^2+k^2}}$). Further inspection of Eq. 5 suggests two extremes for the response of the pool size for variations in the input flux (Fig. 2B). If the turnover time of the pool (τ) is short (i.e. k is large) relative to the frequency of oscillation of the input flux (ω), the pool size will vary almost directly in proportion to the input. However, if the turnover time of the pool (τ) is large (i.e. k is small) relative to the frequency of oscillation of the input flux (ω), the response of the pool size to variation in the input will be relatively small (Sarmiento and Gruber 2006). In summary, for cyclical changes or short-lived pulses,

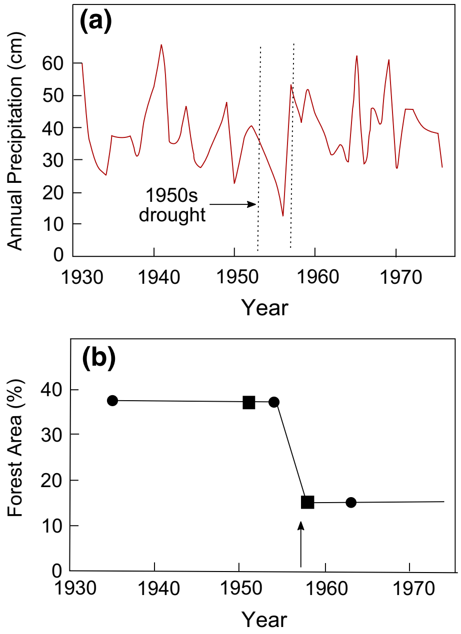


Fig. 3 Buffering of inputs that vary in time: Water inputs from the atmosphere vary in time over several decades in a *Pinus ponderosa* forest in New Mexico, USA (**A**). The ecosystem buffered the inputs over several decades through storage leading to a stable forest size (**B**). However, large variations in the water inputs in the 1950s exceeded the buffer capacity of the ecosystem causing a strong decreased in the forested area (changed after Allen and Breshears 1998)

buffering is manifest in the magnitude of system response relative to input forcing.

Besides cyclical changes, the input to an ecosystem might also change in a stepwise manner. Let us assume a pool with pool size M_0 and input flux Q_{in} is in steady state ($M_0 = Q_{in}/k$). As the input flux changes stepwise from Q_{in} to Q'_{in} the pool changes to a new steady state with a new pool size $M_1 = Q'_{in}/k$, and the pool size changes according to:

$$M(t) = M_1 - (M_1 - M_0) \cdot e^{-kt} \tag{6}$$

where t is the time since the change of input. The response time, defined as the time required to reach a new steady-state after a change in inputs is proportional to 1/k, or the turnover time of the system in the initial state. In this simple one-box formulation, both well- and poorly-buffered systems will attain the same new steady-state pool size. However, well-buffered systems have longer response times. Figure 2D displays the development of a pool M for various values of k in response to a stepwise and permanent halving of the input flux Q_{in}, shown in Fig. 2C. The example illustrates that the response of the pool and the extent to which this response is dampened compared to the change over time of the input flux depends on the pool´s initial turnover time.

The concept is readily extendable to multi-compartment systems defined by a system of ordinary differential equations, as illustrated in the following example. Figure 2F shows the temporal development of three connected N and P pools (soil, plant biomass, and litter layer) in a forest following a stepwise fivefold increase in the rate of N and P deposition to the litter layer (Fig. 2E) while all other inputs of P (i.e. weathering) and N (i.e. N_2-fixation) to the ecosystem being held constant. Changes of the N and P pools in Fig. 2F are normalized to the initial pool size. In this example, the P-pools require ~ 2500 years to attain a new steady state. A k value for P for the whole system, derived from fitting Eq. 6 to the sum of biomass in all pools, is 0.002 year^{-1}. In contrast, N-pools achieve a new steady state after about 500 years, with a k value for the whole system of 0.01 year^{-1}. In this example, the P cycle is more strongly buffered than the N cycle and thus reacts more slowly to a change in inputs.

Simple example: storage of water in ecosystems buffers time-variable inputs

In "Buffering of inputs in ecosystems: quantitative framework" section we defined the terms buffering, buffer capacity as well as buffer pool (Box 1 part A) and introduced a simple model. In the following, we will illustrate how storage can buffer temporally varying inputs over short to intermediate timescales, based on a simple example.

Ecosystems can buffer water inputs that vary in time through water storage (Singh et al. 1998; Fernandez-Illescas et al. 2001; Porporato et al. 2002; Viola et al. 2008). For example, Mediterranean ecosystems experience drought in summer when solar radiation and temperature are high, and a surplus of water in winter when precipitation rates are high and solar radiation and temperature are lower (Viola et al. 2008; Lauenroth et al. 2014). The capacity of these ecosystems to buffer low external water inputs depends on the buffer pool, i.e. on the size of the pool of water stored in plants and soil and the turnover time of the water pool relative to the magnitude and frequency of rainfall cyclicity (Fig. 2). If the turnover

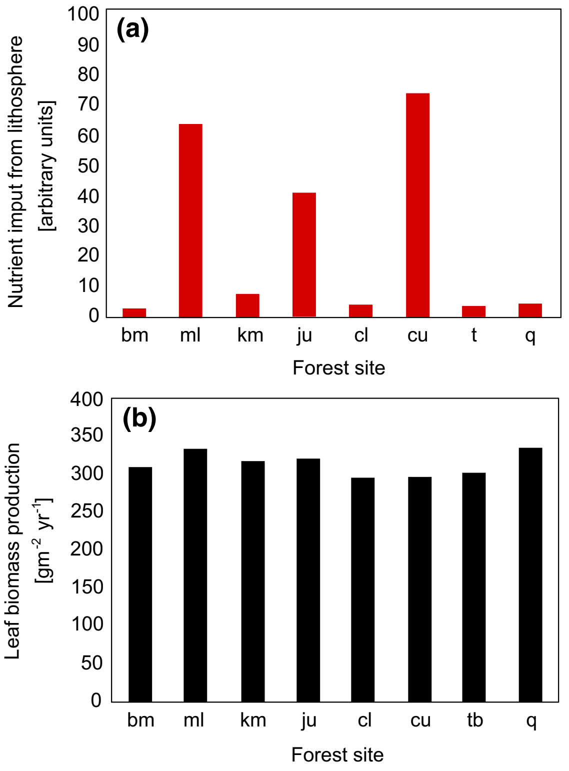


Fig. 4 Buffering of inputs that vary in space: nutrient inputs from the lithosphere differ largely between nine *Fagus sylvatica* forest sites in Northwest Germany on different bedrock (**A**). The ecosystems buffer the nutrient inputs through nutrient storage and recycling, leading to very similar productivities across the nine ecosystems (**B**). The labels on the x axis indicate the bedrock of the nine sites (changed after Meier et al. 2005)

time of the water pool in the ecosystem is large relative to the oscillation frequency of the water input, the size of the water pool changes little over time, and the system is well buffered. However, if the turnover time is small relative to the oscillation frequency, the size of the storage pool changes considerably over time and might even change proportionally with the input flux (Fig. 2).

If the period of oscillation of the inputs by far exceeds the turnover time of the storage pool, the ecosystem might cross a tipping point by fundamentally changing its structure and functioning (Scheffer et al. 2001; Zehe and Sivapalan 2009). For example, Allen and Breshears (1998) studied forests in New Mexico that buffered small changes in annual precipitation for many decades (Fig. 3) until a severe drought occurred that caused a rapid shift of the ecotone, i.e. the border between two biomes (Fig. 3). The ecotone between semiarid ponderosa pine (*Pinus ponderosa*) forest and piñon–juniper (*Pinus edulis* and *Juniperus monosperma*) woodland shifted extensively (≥ 2 km) and rapidly (< 5 years) through mortality of *Pinus ponderosa* in response to an extended period of decreased precipitation (Fig. 3). This shift persisted for decades and was accompanied by accelerated soil erosion in areas previously vegetated by pine forest. Thus, in this example, the ecosystem buffered temporally varying water inputs for many decades until the water input was too small and the capacity of the ecosystem to buffer transiently low water inputs was exceeded, which shifted the structure of the ecosystem.

Buffering of variable inputs through storage and recycling of elements

Buffering and recycling

In the previous section we developed an example illustrating the functioning of a buffer pool. In this one-pool example the buffer pool was the water stored in the ecosystem, and the ecosystem could buffer short and intermediate-term decreases in water inputs. Decreased inputs over long periods cannot be buffered only by storage because the buffer capacity (Box 1 part A) would be quickly exceeded (see above). Buffering of low inputs over long periods only works if the buffer is re-filled by recycling (Fig. 1 dark blue text and arrows), i.e. by ecosystem-internal fluxes (Box 1 part B). This can happen at the scale of a single plant through element resorption or at the scale of the ecosystem through re-uptake of elements (Fig. 1). Recycling retains elements in the ecosystem, and thus maintains the buffer, as we will explain through three examples.

Buffering through storage and recycling of elements: three examples

As a first example, tropical lowland forests on highly weathered soils receive a large proportion of nutrients that sustain their primary production from the atmosphere in the form of dissolved ions and dust (Fig. 1 top left; Chadwick et al. 1999; Carrillo et al. 2002). These inputs are highly variable in time (Kellman et al. 1982; Carrillo et al. 2002). Despite the low

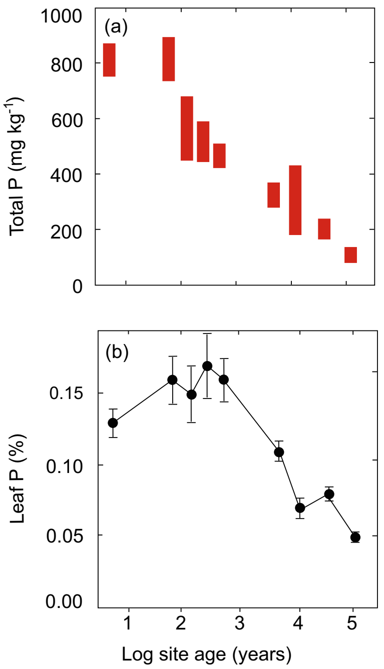


Fig. 5 Soil total phosphorus (P) stocks decrease during ecosystem development in the Franz Josef chronosequence in a glacier foreland in New Zealand as a result of low net inputs to the ecosystem (**A**). During intermediate stages of development, the ecosystem buffers decreased P inputs (compared to the initial stages) by storage and recycling, and thus leaf P contents are still as high as during the initial stages (**B**). However, at late stages of ecosystem development (> 5000 years), the buffer capacity is exceeded and leaf P contents are very low (**B**) (changed after Richardsson et al. 2004)

atmospheric inputs and their high temporal variability, tropical lowland forest ecosystems have high rates of net primary production that are similar to upland tropical forests which receive larger inputs of nutrients from bedrock (Vitousek and Sanford 1986). The reason for this is that they recycle nutrients very efficiently and store large amounts of elements in the biomass (Vitousek and Sanford 1986).

As a second example, European beech (*Fagus sylvatica* L.) forests exist on a large range of geological substrates, and thus the nutrient inputs that these ecosystems receive from bedrock (i.e., inputs from lithosphere, Fig. 1) differ largely among different beech forests (Fig. 4). Despite differences in nutrient inputs from the underlying substrate, productivity among mature *beech* forests growing on different substrates under the same climate conditions is very similar (Fig. 4; Meier et al. 2005). This is because productivity is largely supported through recycling of nutrients in the plant and in the entire ecosystem. Processes of nutrient recycling and storage allow plants to thrive at sites with minimal nutrient inputs (Chapin et al. 1990; Millard and Grelet 2010). Without efficient recycling, storage pools of nutrients would be quickly depleted if nutrient inputs from the bedrock were constantly low. In contrast to the former (tropical forest) example, the nutrient inputs in the latter (beech forest) example (Fig. 4) differ in space (see also Box 1 part A) and the buffering behavior of a beech forest is deduced from a comparison of the biomass production rate of different forest ecosystems.

As a third example, after a disturbance (e.g. fire, or drought) or during interglacial periods, ecosystems undergo a primary succession and subsequently a retrogressive succession during which ecosystem productivity and plant biomass production decrease (Birk and Birk 2004; Wardle et al. 2004). The reason for this decrease is that the total nutrient pool as well as available and intermediately available nutrient pools in soil decrease over time due to the cumulative export of nutrients (decreased net inputs, Fig. 2C and D) and formation of plant-unavailable nutrient pools (Walker and Syers 1976; Richardson et al. 2004). During intermediate stages of ecosystem retrogression, storage and recycling can still buffer decreased P inputs. This can be observed, for example, in the chronosequence at the Franz Josef glacier in New Zealand (Fig. 5). At sites where the glacier retreated 130–5000 years ago, the leaf P content is as high as the very young sites, despite strong decreases in soil P. This observation suggests that recycling of P buffers the decreased net P inputs and P availability (Richardson et al. 2004). In contrast, at the older sites (> 5000 years) leaf P content strongly decreased compared to younger sites because the capacity of the system to buffer low inputs was exceeded.

The study of buffering in ecosystems through storage and recycling of elements is associated with the challenge that stored elements, in contrast to water (see "Simple example: storage of water in ecosystems buffers time-variable inputs" section), often need to be mobilized before they can move from one ecosystem pool to another. For instance, adsorbed ions in soil must be desorbed to become available for plant uptake and nutrients covalently bound in soil organic matter (SOM) must be mineralized. Mobilization of elements from storage pools both in the plant and in the soil can be very slow, and might limit the capacity of the ecosystem to buffer the effects of variable inputs on ecosystem properties, such as primary production. Thus, the major challenges in the study of buffering through storage and recycling of elements are: (a) the identification and quantification of the buffer pool; (b) the determination of the rate at which elements of the buffer pool are mobilized; and (c) the determination of the rate of element recycling.

In the following sections, we review the current knowledge of processes of storage and recycling that allow ecosystems to buffer element inputs. To start with, we synthesize the current knowledge of element storage in plants (4.1) and soils (4.2).

Storage of elements in ecosystems

Storage of elements in plants

Plants store C and nutrients as reserves, which are storage pools that can be mobilized by plants (Fig. 1). The build-up of reserves in the plant can compete with other plant functions, such as growth or defense, and allows the plant to: (1) overcome periods of asynchrony between supply and demand, e.g., nighttime metabolism; (2) recover from damage and biomass loss via herbivory, disturbance, or disease; and (3) support sudden changes in allocation patterns during plant development, like the shift from vegetative to reproductive growth (Chapin et al. 1990). The most abundant storage form of C in plants is carbohydrates, i.e., sugars and starch. These reserves can make up a substantial proportion of dry biomass in leaves, branches, and roots in trees (Hoch et al. 2003; Wurth et al. 2005) and provide a buffer large enough to regrow the entire tree foliage four times (Hoch et al. 2003). Carbohydrate concentrations are, on average, highest in leaves (14%) and roots (10%) and lowest in stems (7%). Starch stored as osmotically inactive grains in chloroplasts, or in specialized organelles called amyloplasts, makes up roughly half of the carbohydrate pool (6, 7, and 3% in leaves, roots and stems, respectively, Martínez-Vilalta et al. 2016). Inorganic nutrients like Mg, S, K or P as well as amino acids and proteins, are typically stored and withdrawn from vacuoles with specialized membrane pumps or molecule carriers. Lipids are concentrated in specific organelles called oleosomes, spherical bodies in the cytoplasm of parenchyma cells that self-organize due to the polar nature of the fatty acids (Mohr and Schopfer 1995). All of the previously described storage compounds can individually be thought of as pools such that the concepts presented in “Conceptual framework” section and Box 1 for changes in pool size are applicable.

The mobilization of reserves can buffer resource supply during unfavorable environmental conditions and extreme events (e.g., drought, fire, Fig. 3) when photosynthetic activity and root uptake is constrained by water or nutrient shortages (Gessler et al. 2017). While most soluble carbohydrates can be readily re-fed into the metabolic pool, starch must be hydrolyzed to glucose before it can be metabolized or transported, and more complex or large molecules like lipids must be converted to other forms like carbohydrates before they can be transported to other plant organs through the phloem (Mohr and Schopfer 1995). The mobilization of reserves occurs over diurnal scales in developing leaves (Gibon et al. 2004; Stitt and Zeeman 2012) but can also span across seasons (Helle and Schleser 2004), decades or even centuries (Wiley and Helliker 2012). Plant reserve formation and reserve use is a highly variable component of ecosystem element storage and is governed by plant control mechanisms that are currently not well understood (Huang et al. 2018). What is known is that short-term (e.g., daytime) storage of carbohydrates in starch granules and their mobilization during nighttime is genetically controlled (Gibon et al. 2009) and can prevent C shortages in growth and other metabolic activities (Smith and Stitt 2007). The regulation of long-term C storage activity and the factors determining the amount of storage in long-lived organisms like trees is still not fully understood (Dietze et al. 2014; Hoch 2015) but is thought to optimize fitness via long-term survival (Wiley and Helliker 2012; Muhr et al. 2013, 2016).

Accumulation of carbohydrates may occur when growth is constrained by unfavorable environmental conditions such as low temperatures or drought (Körner 1998, 2003; Muller et al. 2011). Other evidence suggests that source activity (photosynthesis) is downregulated when sink activity (e.g., growth, respiration) is constrained. For example, when developing fruits are removed from a branch (Nebauer et al. 2011) the entailing build-up of carbohydrates triggers a sugar sensing feedback mechanism that causes a molecular down-regulation of photosynthetic rates

(Koch, 1996). The uptake of mineral nutrients is generally regulated by the demand of the plant for growth and development, but accumulation of nutrients may also occur at the same time (Wirén et al. 1997). Research on the regulation and control mechanisms of nutrient uptake and accumulation has so far focused mainly on crops (Yu et al. 2015) and very little information is available for natural ecosystems. Uncertainties in our knowledge of nutrient uptake and accumulation are a research frontier that is important for developing a holistic perspective of buffering in plant–soil ecosystems.

The capacity of plants and trees to drawn down, i.e. fully exploit, C reserves is also not well understood and is an active field of research (Hartmann and Trumbore 2016). During periods of C limitation from shading, trees can use up to ~ 85% of stored carbohydrates before they die (Weber et al. 2018). In contrast, some species can switch to other resources like lipids to postpone starvation (Fischer et al. 2015). However, mobilization of stored carbohydrates is inhibited by declining hydration during drought (Hartmann et al. 2013a) in above-ground tissues, but less so in the root system (Hartmann et al. 2013b; Li et al. 2018). While draw down of carbohydrates during drought is a common phenomenon, it is not ubiquitous across different species, functional types, or even organs (Adams et al. 2017).

In summary, plants can store large amounts of C and nutrients in the form of reserves that are sufficiently large to allow regrowth of the entire tree foliage several times (Fig. 1). However, mobilization of stored carbohydrates can be inhibited by declining hydration during drought, and the processes of storage mobilization and draw down are not yet fully understood. Future research should study how storage pools in plants are related to cyclical changes in inputs and to which extent the response in plant biomass production is dampened and delayed in response to changes in inputs (see "Conceptual framework" section, Box 1).

Storage of elements in soils

Soils can store nutrients released from weathering of primary minerals or derived from the atmosphere in inorganic form and bound in SOM (Fig. 1). Nutrients are retained in soil due to sorption on charged surfaces. Surface charges of the solid soil phase can be either permanent or variable, i.e. pH-dependent (Essington 2003). Most of the charge in soils is negative and is balanced by cations including protons. However, significant positively charged mineral and organic colloid surfaces can be found in acidic soils with dominant variable charge (e.g., Oxisols) (Bergaya et al., 2006). Globally, in neutral and alkaline soils Ca^{2+} is the dominant exchangeable cation (25.18 ± 16.28 $cmol_c\ kg^{-1}$), followed by Mg^{2+} (10.06 ± 8.49 $cmol_c\ kg^{-1}$), Na^+ (1.21 ± 4.31 $cmol_c\ kg^{-1}$), K^+ (0.737 ± 0.684 $cmol_c\ kg^{-1}$) (Essington 2003). With increasing levels of leaching, soil pH and base cation contents decrease, and the relative proportion of Al^{3+}, Mn^{+2} and K^+ in the exchange complex increase Essington 2003; Jobbágy and Jackson 2001; Li and Johnson 2016). Despite the fact that exchangeable cations and anions for many lithogenic elements represent only a minor fraction of the total soil nutrient element inventory, the temporal retention and demand-driven release of these nutrients from the exchange complex is one of the main process facilitating storage and recycling of nutrients in ecosystems (Fig. 1 light blue text and arrows) and sustain the productivity of terrestrial ecosystems (Sverdrup and Rosen 1998).

Total soil cation and anion storage and the relative proportion of sorbed ions can vary significantly throughout the seasons mostly because of changes in plant uptake, atmospheric inputs, leaching rates, and SOM mineralization dynamics Helmisaari and Mälkönen 1989; Nodvin et al. 1988; Vitousek and Reiners 1975). Similarly, decadal-scale changes in the total, and the composition of sorbed, nutrients has been observed during forest succession (Johnson et al. 2008). More dramatic changes in sorbed ions and nutrient leaching losses occur as a result of large ecosystem disturbance like soil degradation (Fang et al. 2017), forest clearcutting (Nodvin et al. 1988), and fire (Fang et al. 2017; Ulery et al. 2017).

While the stocks of sorbed elements in soils have been quantified extensively, much less is known about the rates at which elements sorbed to different minerals desorb and become available to biota under field conditions. This process might be limiting for plant nutrition. Plants and microorganisms can mobilize sorbed ions by enhancing their desorption from mineral surfaces. They do this by releasing protons that exchange with sorbed cations or by releasing organic anions. Organic anions can both exchange with sorbed anions and chelate cations, preventing precipitation of cations with nutritive anions (Hinsinger 2001; Richardson et al. 2009). Despite release of organic acid by microorganisms, nutrients might only desorb at low rates from mineral surfaces. It has been shown, for instance, that desorption of P from goethite is very slow compared to the release of P from primary minerals (Pastore et al. 2020) and might limit plant P uptake if P bound to goethite is the only P source (Klotzbücher et al. 2020).

Besides being sorbed on charged surfaces in inorganic form, N and P can also be stored covalently bound in SOM. Soils have a finite capacity to sequester SOM, and thus nutrients in organic form, with the maximum amounts depending on climate and soil characteristics (Jackson et al. 2017). The factors that control the stabilization of OM in mineral soil against decomposition have been intensively studied in recent years. The emerging picture is that OM is mainly stabilized through adsorption to charged mineral surfaces (organo-mineral interactions) and through occlusion, both making OM spatially inaccessible for microorganisms and exoenzymes (Dungait et al. 2012; Schmidt et al. 2011). Support for this concept comes from studies showing that organic C in microaggregates (John et al. 2005; Monreal et al. 1997) and in mineral-associated fractions (Anderson and Paul 1984; Ludwig et al. 2003; Bol et al. 2009) is older than the mean age of organic C in soil. Nutrients covalently bound in OM are highly relevant for plant nutrition because they are mineralized at intermediate timescales (see "Recycling of elements in terrestrial ecosystems" section). Nitrogen in OM comprises more than 95% of all N present in soils (Johnson 1992). The molar C:N ratio of OM in mineral soils ranges on average between 12.2 in desert soils to 36.6 in boreal forest soils (Xu et al. 2013). The C:P ratio of OM is typically much higher averaging around 250 Kirkby et al. 2011; Spohn 2020a, b) but is more variable among ecosystems than the C:N ratio (Kirkby et al. 2011; Tipping et al. 2016; Xu et al. 2013). The C:P ratio and to a lesser extent the C:N ratio of OM decrease during decomposition (Cotrufo et al. 2013; Spohn and Chodak 2015; Zechmeister-Boltenstern et al. 2015). This enrichment of N and P over C is likely driven by interactions of the charged N- and P-containing OM moieties with charged mineral surfaces, which stabilizes nutrient-rich OM against decomposition Knicker 2011; Newcomb et al. 2017; Cotrufo et al. 2019; Spohn 2020a,b).

Storage of elements in soils is also controlled by erosion, transport, and deposition of soil. Hillslope erosion preferentially transports topsoil, and thus elements that are present in larger concentrations in the topsoil, such as organic C, N and P (Avnimelech and McHenry, 1984). Thus, soils in areas affected by soil erosion are often depleted in organic C, N and P, whereas in depositional environments, soils are enriched in organic C, N, and P (Jobbágy and Jackson, 2001; Berhe et al. 2018). Studies that support this finding and identify the topographic control on the spatial variability of element storage in undisturbed natural systems are limited (for exceptions see Avnimelech and McHenry, 1984; Yoo et al. 2006; Weintraub et al. 2015). However, it has been shown, that depositional environments such as floodplains have increased OC stocks compared to sites of erosive soil losses (van Oost et al. 2007; Oost et al. 2012; Hoffmann et al. 2009; 2015; Berhe and Torn 2016; Wang et al. 2017). Furthermore, soil erosion depends not only on climate and topographic slope, but also on vegetation cover (e.g., Starke et al. 2020; Schmid et al. 2018). Finally, bioturbation in the upper ~ 0.5 m of soils (Schaller et al. 2009, 2018) that leads to the translocation of OM from the topsoil to the subsoil might increase storage of organic C, N and P since decomposition of OM in the subsoil is slower than in topsoil due to interaction with non-saturated mineral surfaces in the subsoil (Don et al. 2008; Jackson et al. 2017).

Taken together, soils retain nutrients in both organic and inorganic forms (white boxes in Fig. 1), which is strongly affected by soil minerals and topography. The soil nutrient pools can be sufficient to supply plants for several decades with nutrients. However, the mobilization of nutrients stored in soil might limit plant nutrient uptake. Future research should study how different soil types and storage pools in soils respond to (cyclical) changes in inputs, and to which extent their response to periodic changes in inputs are dampened and delayed (see "Conceptual framework" section).

Recycling of elements

Ecosystems do not only store nutrients, as discussed above, but also recycle nutrients, which maintains them in the ecosystem and can compensate for low inputs. In this section, we review the status of knowledge of element recycling, first, in plants through resorption of nutrients ("Recycling of elements in plants" section) and second, in ecosystems through re-uptake of elements by plants that have been used by plants before ("Recycling of elements in terrestrial ecosystems" section).

Recycling of elements in plants

Plants recycle nutrients internally as they resorb nutrients from senescent leaves and roots before abscission and transport them to other plant tissues where they are re-used (Fig. 1) (Aerts 1996; Yuan and Chen 2009; Vergutz et al. 2012). Based on a global meta-analysis, Vergutz et al. (2012) concluded that terrestrial plants resorb 70.1% of leaf K, 64.9% of leaf P, and 62.1% of leaf N before leaf abscission, while only 28.6% of leaf Mg, 23.3% of leaf C, and 10.9% of leaf Ca is resorbed. Graminoids tend to have the highest nutrient resorption, whereas deciduous angiosperms typically resorb a comparatively small proportion of their leaf nutrients (Vergutz et al. 2012). The differences in nutrient resorption between graminoids and deciduous angiosperms amount to about 14% for C and N and to 5–6% for P and K (Vergutz et al. 2012). However, it has to be taken into account that K resorption might be overestimated in Vergutz et al. (2012) because K leaches very quickly out of senescent leaves (Schlesinger 2020). Nutrient resorption from senescent leaves is not only affected by plant functional type but also by mycorrhizal symbiosis; P resorption was 76% larger for ectomycorrhizal trees than for trees forming symbiosis with arbuscular mycorrhiza (Zhang et al. 2018). In contrast to nutrient resorption from leaves, much less is known about nutrient resorption from senescent roots (Fig. 1). Available data indicate that resorption from roots is lower than from leaves (Brant and Chen 2015) but does not allow for conclusive statements. Other studies have found that resorption of N from senescent leaves generally increases with increasing latitude and decreases with increasing mean annual temperature (MAT) and mean annual precipitation (MAP) across different plant functional types. In contrast, resorption of P decreases with latitude and increases with increasing MAT and MAP (Yuan and Chen 2009; Reed et al. 2012). This pattern has been attributed mostly to the low P and high N availability in tropical soils and low N availability in boreal soils (Yuan and Chen 2009; Reed et al. 2012).

The extent to which plant species resorb nutrients from senescent leaves correlates with the nutrient status of the leaves. Vergutz et al. (2012) showed based on observational data that the percentage of resorbed N, P, K, and Mg each decline with increasing leaf N, P, K, and Mg concentration, respectively. This indicates that plants adjust the efficiency with which they resorb nutrients to the nutrient concentration in their leaves. Since these results are derived from observational studies and all species only grow on a limited number of soils, it cannot be concluded whether this is due to an adaptation of the species to the nutrient availability of the soils in which they typically grow or due to an adjustment of individual plants to the local nutrient availability. A meta-analysis of fertilization studies showed that individual plants are to some extent able to adjust the proportion of nutrients they resorb from senescent leaves within only one growing season. N resorption decreased in response to N fertilization on average by 12.2% across different plant functional types, while P resorption decreased following P fertilization by 8.8% (Yuan and Chen 2015). These experimental results show that individual plants can adjust nutrient resorption efficiency over short timescales to adjust to nutrient availability of the soil in which they grow. This plasticity allows plants to use nutrients more conservatively under nutrient-poor conditions and to save the energy required for resorption when soil nutrient availability is high (Chapin et al. 1990, 1990; Yuan and Chen 2015). Based on a global dataset it was shown that N resorption in woody plants depends on both the N content and the P content of the leaves, and vice versa, P resorption is controlled by both P and N content of leaves (Han et al. 2013). This finding indicates that the resorption of one element depends not only on the concentration of the element in the leaves but also on the leaf contents of other nutrients. In the example of the chronosequence in New Zealand (Fig. 5) resorption of P allowed plants to maintain relative high leaf P contents in the intermediate stages of ecosystem development (Richardson et al. 2004). However, the example also shows that the possibility to compensate for low P inputs from soil by P resorption is limited (see Fig. 5).

In summary, the extent to which plants recycle nutrients internally depends on the plant functional type, the plant nutrient status, plant-microbial interactions, and nutrient availability. In general, the resorption efficiency is higher for N, P, and K than for other nutrients. Furthermore, previous studies indicate that resorption of a nutrient is only rewarding for the plant if the availability of the nutrient in the soil is low.

Recycling of elements in terrestrial ecosystems

Nutrients derived from plant litter can be taken up again by plants, and many nutrients cycle several times between soil and plant before eventually being lost from the ecosystem (Fig. 1). In this section, we discuss recycling of nutrients as the re-uptake of plant-litter derived nutrients by plants. Microorganisms might also re-use nutrients that have passed through the soil microbial biomass before. However, since the distinction between re-use of nutrients derived from microbial necromass and microbial cell-internal element re-cycling is difficult and has hardly been addressed so far (Spohn and Widdig 2017), we concentrate our discussion on the recycling of nutrients in ecosystems by plants (dark blue arrows in Fig. 1).

Nutrient recycling at the ecosystem scale encompasses re-use of nutrients within plants (resorption, see "Storage of elements in plants" section) and re-uptake of nutrients contained in plant and animal detritus, such as litter. Nutrients in litter are released in inorganic form during the decomposition process. This process represents one of the prerequisites for recycling since it enables plant uptake of litter-derived nutrients. During decomposition of litter, large organic polymers are depolymerized and organic C, N, P, and S are mineralized (Coleman et al. 1983; Richardson et al. 2009). Whether N and P are mineralized or immobilized in the microbial biomass depends on the critical element ratio of the OM (Parton et al. 2007). If the C:N or the C:P ratio of OM is above the critical element ratio, N or P, respectively is immobilized by microorganisms and is not rendered available for plant uptake. If the element ratio of OM is below the critical element ratio for the respective nutrient, the nutrient content of the OM exceeds the microbial nutrient demand and excess inorganic N or P is released, which is termed net mineralization (Parton et al. 2007; Spohn 2016). The threshold C:N ratio for net N mineralization from plant leaf litter was determined to be between 20 and 40 (Gosz et al. 1973; Blair 1988; Parton et al. 2007; Moore et al. 2011; Mooshammer et al. 2012; Heuck and Spohn 2016), while threshold C:P ratios for net P mineralization are between 300 and 1700 (Edmonds 1980; Blair 1988; Saggar et al. 1998; Moore et al. 2011; Heuck and Spohn 2016). The threshold element ratio allows us to estimate if N or P mineralization takes place. However, plants might also take up small amounts of N in the form of amino acids (McKane et al. 2002; Jacob and Leuschner 2015).

The extent to which plants take up litter-derived nutrients can be quantified by either mass balance approaches (Box 1) or by tracing nutrients contained in litter until their uptake by plants through isotopes. Using a mass balance approach, Chapin (1991) estimated, based on long-term measurements of nutrient fluxes, that 96% of both N and P that plants take up in a tundra ecosystem were recycled from plant detritus. In temperate forests, 69–93 and 67–89% of the N and P were derived from plant detritus, and 87–88 and 65–85% of K and Ca, respectively (Chapin 1991; Schlesinger 2020). A mass balance approach was also used by Cleveland et al. (2013). They estimated that globally, recycled N and P (resorption plus re-uptake of plant-litter derived nutrients) contributed ca. 90 and 98%, respectively, to yearly plant N and P demand (Cleveland et al. 2013). Uhlig et al. (2017) deduced that P and K must be largely recycled in temperate forest because the plant P demand was not covered by the P released from bedrock. Based on a similar mass-balance approach, Schuessler et al. (2018) deduced Mg must be largely recycled in a montane rain forest. One large uncertainty in all mass-balance studies is the flux of nutrients from plants to the soil (Fig. 1). The determination of this flux is not trivial because it requires information not only about the nutrient content in different plant compartments but also about the turnover of the different plant compartments and about nutrient resorption from the different plant compartments (Sec. Recycling of elements in plants).

The contribution of litter-derived nutrients to plant element uptake can more directly be assessed through isotopic tracer studies. For example, the addition of ^{15}N-enriched plant litter and the subsequent recovery of ^{15}N in plants can be used to estimate the magnitude of recycling for plant N uptake. In contrast to the large contribution of recycling to plant N uptake reported above based on an indirect mass-balance approach, all studies tracing the fate of leaf-litter derived N based on isotopes report surprisingly small recoveries in above- and below ground plant biomass irrespective of experimental duration (up to eleven years): $< 5\%$ in forests (Zeller et al. 2000, 2001; Stoelken et al. 2010; Guo et al. 2013b; Leppert et al. 2017) and grasslands (Seeber et al. 2008; Saj et al. 2009). The small ^{15}N tracer recovery in plant biomass in direct approaches might be related to: (1) long-term storage of N-rich organic matter in soils (see "Storage of elements in plants" section); (2) methodological constraints, namely the non-homogeneous distribution of the ^{15}N label; and (3) the importance of root rather than leaf litter (Schmidt et al. 2011; Guo et al. 2013a; Ruppenthal et al. 2015) for element recycling, which is not accounted for in studies adding ^{15}N-labeled leaf litter. Similar to N, several authors suggested that the main proportion ($> 90\%$) of P taken up by beech trees originates from the organic layer (Brandtberg et al. 2004; Jonard et al. 2009; Hauenstein et al. 2018). The critical role of the organic layer for plant uptake was also reported for Mg but not for Ca (van der Heijden et al. 2014; Heijden et al. 2015). In agricultural systems, a maximum of 44% of P taken up by plants originated from plant residues (Noack et al. 2014; Maltais-Landry and Frossard 2015).

Irrespective of the element considered, probabilistic models predict that the contribution of recycled nutrients to plant nutrition is linked to the rates of external input into an ecosystem. (Spohn and Sierra 2018). This follows from simple probability distributions; the lower the rate at which a given nutrient enters the ecosystem from outside (i.e., from the atmosphere or the bedrock) in comparison to the rate at which the nutrient is released from plant detritus, the higher the probability that the plant takes up an atom that has already passed at least once through the plant biomass.

In conclusion, indirect and direct approaches concur that N and P are heavily recycled in all ecosystems to cover the plant nutrient demand. Both direct and indirect approaches suggest that recycling is of less importance for Mg and K, while no conclusive statement can be drawn for Ca.

Caveats and future research needs

In this contribution, we revisited concepts of buffers in environmental sciences, developed a conceptual framework of buffering of inputs in terrestrial ecosystems, and reviewed the current knowledge about storage and recycling of elements in plants and ecosystems (Fig. 1). In this section, we address research needs in this field of study.

First, here we propose studying ecosystem responses to resource inputs as dependent on storage and recycling of elements. Since buffers dampen the effect of an input, one of the challenges when studying buffering in ecosystems is the clear distinction between cause and effect. For example, biomass production (often used to evaluate the buffering of an ecosystems (see Fig. 4)) depends on many different inputs to the ecosystem. Thus, it is difficult to determine the contribution of element storage and recycling to ecosystem functioning. In addition, it is challenging to unambiguously attribute changes in ecosystem functioning to changes in external inputs, unless they are as extreme as in the case of the drought example (Fig. 3). In order to understand the contribution of storge and recycling to ecosystem functioning, long-term observations of ecosystems are required (Lindenmayer et al. 2010; Richter et al. 2018) in combination with tracer analyses, e.g. isotopes, that capture the long-term fate of elements in ecosystems.

Second, this review suggests that the buffer capacity (see Box 1) can be limited not only by the size of storage pools in an ecosystem, but also by the capacity to mobilize stored elements. The rate of mobilization can be critical for the ability of ecosystems to dampen and delay their response to temporally varying external inputs. The boreal forest is an example of an ecosystem in which an element is stored in large quantities and at the same time primary production is limited by the same element. Boreal forests store large amounts of N in the organic layer, but with increasing ecosystem development time the ecosystem is increasingly unable to mobilize it (Peltzer et al. 2010). Future research should focus on the processes by which stored elements are mobilized and under which conditions available storage (i.e. reserves) become unavailable for organisms.

Third, here we only reviewed knowledge about buffering through storage and recycling of elements. Terrestrial ecosystems can also buffer variations in external inputs to some extent by adjusting nutrient- (and water-) use efficiencies. Plants can, for example, increase the efficiency with which they use a specific nutrient for biomass production when nutrient availability is low. Nutrient-use efficiency is very well described for crops but less so for plants in natural ecosystems (Hawkesford et al. 2016). Future research should quantify to which extent adjustment of nutrient- (and water-) use efficiency allows ecosystems to buffer variation in external inputs.

Fourth, the output flux (Q_{out}) from an ecosystem does not have to linearly depend on the pool size, as assumed here (Fig. 2). Element release from a pool can be dependent on the specific process and not just pool size. For example, ecosystem disturbances (e.g. fires, increased herbivory) are stochastic events (independent of pool size) that can result in rapid output fluxes from the system and likely a different system response than illustrated in this study. An opportunity for future work is to explore how changes in the formulation of the input and export fluxes driven by different climate, geomorphic, or episodic events affect the buffering behavior of ecosystems.

Fifth, future research should explore how storage of water and nutrients in soil and plants affects weathering and nutrient inputs from the lithosphere (Fig. 1). During the last decades, biota have been regarded mostly as drivers of weathering that can cause weathering rates several magnitudes larger than abiotic processes (Finlay et al. 2020). Yet, biota in ecosystems could also decrease weathering rates by reducing the amount of water available for rock weathering. Furthermore, storage and recycling of nutrients by biota can decrease their need to acquire new nutrients from rock. Thus, future studies should explore how weathering rates in different ecosystems change over time depending on storage and recycling of nutrients.

Conclusions

We presented the state-of-the-art in storage and recycling of elements in ecosystems and provided a framework for studying ecosystem responses to element inputs. This approach improves our understanding of the extent to which ecosystems minimize their sensitivity to changes in inputs. In contrast to the concept of resistance, the framework developed here facilitates a process-based understanding of the property of ecosystems to decrease their reliance on external inputs. The approach presented related ecosystem responses to inputs to tangible pools and associated fluxes. This resulted in the testable prediction that ecosystems with large internal storage pools relative to their supply rate and effective recycling of nutrients, buffer external inputs more effectively. Thus, our approach provides a metric for explaining and predicting ecosystem functioning. We suggest, based on this framework, that future research should further formalize ecosystem responses to changes in mass inputs and outputs from above, below, or across the Earth's surface and link these inputs to storage and recycling of elements. Furthermore, future research should identify the boundaries of element recycling in ecosystems since they are ultimately decisive for the time over which ecosystems can buffer external inputs. The conceptual framework presented here improves our ability to predict the responses of ecosystems to environmental change. This is urgently needed to better describe the safe operating space for human existence on our planet and to define thresholds which must not be exceeded to guarantee ecosystem functioning.

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Declarations

Conflict of interests The authors declare no conflict of interest.

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