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Linking chronosequences with the rest of the world: predicting soil phosphorus content in denuding landscapes

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Abstract Results from chronosequences from the arctic to the tropics show that phosphorus (P) availability, total P, and the fraction of bedrock-derived P remaining in soil diminishes as soils age. Thus we predict that ecosystems mantling old substrates are likely to have low available P. Yet there are myriad examples in the biogeochemical literature where the results from chronosequences are used to argue the reverse, and ecosystems observed to be P poor are assumed to mantle an old substrate. This premise is difficult to test, for while the concept of substrate age is useful on uneroded surfaces that formed at a particular time, it becomes obscured in denuding landscapes, where substrate ages instead reflect the rates of rock weathering, denudation and mixing of dust into soil. Here we explore this premise as it relates to one of the most ubiquitous assumptions in the biogeochemical literature: that the differences in nitrogen (N) and P cycling between temperate and tropical regions are driven by gradients in substrate age. We build a conceptual framework for quantifying the fraction of parent material P remaining in soil ([SoilP]/[RockP]), by estimating P inputs (rock weathering and dust deposition) and outputs (P leaching). We parameterize our model with spatially explicit (0.5°) estimates of global denudation, weathering zone thickness, and P deposition. To test the assumption that latitudinal gradients in P status are the result of soil age, we apply a single P loss rate, derived from a humid tropical system in the Hawaiian Islands, to our spatially explicit map of soil residence times. Surprisingly, in this formulation, we find only a modest latitudinal gradient in soil P depletion, with mean depletion values in the humid tropics $<2\times$ greater than in the previously unglaciated humid temperate zone. This small latitudinal gradient in P depletion is unlikely to be sufficient to drive the observed differences in tropical vs. temperate ecosystem stoichiometry (e.g. trends in foliar and litter N:P). Thus our results suggest that, to the extent P depletion is greater in the tropics, the appropriate conceptual model for attributing causation may not be one of a chronosequence where time is the primary driver of P loss. We hypothesize that the covariation of inferred P availability with latitude may be strongly controlled by latitudinal changes in rates of P leaching and occlusion, rather than gradients in substrate age.

Keywords Phosphorus · Soil age · Chronosequence · Tropics · Soil depletion · Weathering · Erosion · Denudation

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Introduction

Soil nutrient status is at the heart the human agricultural enterprise (Sanchez 1976, 2002), and helps shape biological diversity (Tilman 1987; ter Steege et al. 2006) and ecosystem responses to climate change (Nadelhoffer et al. 1999; Shaw et al. 2002). Yet nutrient availability, particularly phosphorus status, is notoriously hard to predict a priori. Soil classification does not include P fertility (USDA-NRCS 2004), and other commonly measured soil properties are not always well correlated with P status (Sanchez et al. 2003; Burkitt et al. 2006). Decades of biogeochemical research have shown that soil age (Vitousek 2004), climate (Chadwick et al. 2003), parent material (Castle and Neff 2009), organisms (Lovett et al. 2004), topography (Porder et al. 2005) and humans (Sanchez 2002) shape the fertility of soils, as long predicted by theory (Jenny 1941, 1980). Nevertheless, a robust framework for evaluating the relative influence of each of these factors as they vary across space has remained elusive (McBratney et al. 2002), and thus our ability to make predictions about soil fertility and its drivers in a particular place remains limited.

Of the aforementioned state factors (*sensu* Jenny), the time since soil began to form has been studied intensively for its effects on phosphorus (P) stocks and biological availability. Myriad data from chronosequences show increased soil P losses relative to parent material, and lower P availability on older surfaces (Stevens 1968; Walker and Syers 1976; Chapin et al. 1994; Crews et al. 1995; Chadwick et al. 1999; Vitousek 2004; Selmants and Hart, 2010). However, to explicitly test the effects of time on soil and ecosystem properties, chronosequence sites are selected to be flat and minimally eroded, so soil age is approximately the age of the parent material. In most landscapes, however, denudation (the physical and chemical removal of material) decouples the soil and parent material age (Porder et al. 2007), and continuous inputs of exogenous material further make the concept of soil age problematic. Geomorphic "surfaces" are convenient on which to work because the age of the surface can be easily defined as the age of abandonment of, for example, a fluvial terrace, glacial moraine, or marine terrace (and as such have received much study in the chronosequence literature). Yet such features are rare in most landscapes, which predominantly consist of hillslopes and channels over which active transport is continuously accommodated. Thus, over the vast majority of Earth's surface where active transport (rather than geomorphic stability) occurs, how do we measure "time"? This is a key question for biogeochemistry, since soil development and depletion occur over time.

In this paper, we postulate that the rate at which a landscape is lowered by denudation sets the "age" of a soil. As a landscape is denuded, rock is converted to soil, moves through the weathering zone, and in so doing, "ages". The longer it takes material to transit the weathering zone, the "older" the soil will be at the surface, all other factors equal. Additionally dust-derived material may be continuously mixed into the mobile soil, and as such, will modify the "effective" age of the soil. We suggest that by quantifying the residence time of rock and dust-derived elements we can estimate soil "ages" in denuding landscapes, and apply what we have learned from chronosequences to predict how much parent material P has been lost in systems where the time since soil formation is not tied to the age of uneroded geomorphic surfaces.

We focus on soil P status, which is of interest for several reasons: (1) P is commonly assumed to limit primary production in many humid tropical ecosystems. (2) We have only a limited ability to predict the occurrence of P-depleted soils, particularly in the humid tropics where agricultural expansion is transforming the landscape at unprecedented rates, and (3) The response of tropical rainforests to global changes in temperature (IPCC 2007) and N deposition (Galloway et al. 2008) may depend on the relative N and P abundance in soil (Hall and Matson 1999). Our proxy for P status is the total P loss relative to parent material. While over short timescales (days to months) low levels of biologically available P may constrain production, over millennia the loss of parent material P may be a more robust indication of P depletion than losses from putatively biologically available pools, which can rapidly exchange with more recalcitrant forms (Richter et al. 2006; Syers et al. 2008; Vitousek et al., in press).

There is strong evidence that plants cycle P more efficiently at low latitudes (Vitousek 1984; McGroddy et al. 2004; Reich and Oleksyn 2004), suggesting that P may be in relatively short supply in those areas. Latitudinal gradients in soil age are commonly suggested as a driver of this trend, with the predominance of Oxisols and Ultisols in the tropics invoked as supporting evidence. While these soil orders are highly weathered, and thus "old" in a soil science framework (Brady and Weil 2002), they have not necessarily resided a landscape for a long time, since weathering rates can be accelerated by other environmental factors, such as temperature, water balances, and the hydrochemistry of the rock. Furthermore, soils depleted in an element of interest might lack this element because the substrate lithology carries this element in low abundance. For example, some of the most infertile Oxisols are soils derived from P poor parent materials, rather than representing ancient soils that have been long exposed to weathering (Buol and Eswaran 2000). Stating that tropical soils are nutrient poor because they are "old" in the soil science meaning is somewhat of a tautology—old soils are highly weathered because highly weathered soils are defined as old. Implicit in the assumption that evidence from chronosequences can be extrapolated to explain the relative P poverty of low latitude ecosystems is the idea that time, rather than any of other factors that might cause soils to be highly weathered, is the primary driver of P depletion. It is this hypothesis that we test here.

To do this, we built a simple model for evaluating the effects of time on P status across the globe by considering the rates of inputs and outputs of P to each 0.5° pixel of the terrestrial biosphere. We treat bedrock and dust-derived material separately, and calculate (i) the concentration in soil of bedrock-derived P based on the time it takes for bedrock P to reach the soil and (ii) the concentration of dust-derived P in soil from the time dust resides in soil. These two concentrations (which are both derived in part from the separate residence times) are then combined to arrive at the concentration of P in soil. Spatially explicit P inputs from rock weathering and dust deposition are derived from denudation of Earth's surface (Montgomery and Brandon 2002; Hilley and Porder 2008), and GCM-based dust deposition rates (Mahowald et al. 2006). Outputs are calculated based on rates of P leaching from parent material (Vitousek 2004), and initially held constant across regions with a positive annual water balance (Mitchell and Jones 2005). Since we expect processes other than leaching to drive P losses in arid ecosystems we do not consider them further here. In addition, we restrict our analyses to systems that were not glaciated during the last glacial maximum (LGM), since soil residence time in these systems is well constrained and governed by processes beyond those considered in our model. We use this first-order model to test the hypothesis that soils in the humid tropics are more P depleted than soils in humid temperate regions as the result of latitudinal gradients in the weathering time of the substrate. We find that weathering time alone is unlikely to produce the inferred latitudinal gradients in P status, and that latitudinal variations in other factors that control the P leaching rate provide a more compelling explanation for inferred trends in worldwide soil P status.

Methods

Model formulation

P can enter a soil in two ways—the weathering of primary minerals or the deposition of exogenous material (hereafter dust). On a stable geomorphic surface, soil is derived from in situ weathering of the rock, and so the soil and weathering zone deepens over time as weathering proceeds. However, in denuding landscapes, bedrock-derived P is cycled into the soil as the weathering zone moves downward due to denudation (Bern et al. 2005; Porder et al. 2007). As denudation removes material and brings rock into the vadose zone, this rock is converted into saprolite. This saprolite is converted to soil, mixed and disaggregated by biological and geomorphic processes near the surface, and eventually transported away. In the simplest conception, the mean residence time of bedrock-derived material in the soil (t_b; kyr) is a function of the weathering zone thickness (Z; m), soil thickness (Z_s; m), denudation rate (ε; m kyr^{-1}), and the propagation rate of the weathering front into fresh rock (ε_w; m kyr^{-1}) (Fig. 1). If the weathering zone is thicker than the soil, mass may be leached from the saprolite before it is ever biologically relevant.

The amount of leaching depends on the residence time, as well as a mean leaching rate (L; mol m^{-3} kyr^{-1}), which likely depends on the element of interest, climate (Porder and Chadwick 2009), soil redox conditions (Chadwick and Chorover 2001; Thompson et al. 2006), the hydrochemistry of the saprolite as it chemically evolves, and the parent

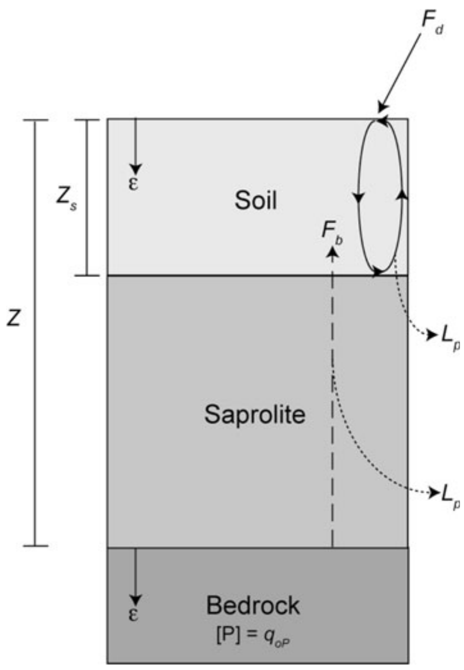

Fig. 1 A schematic illustration of the parameters used in this model

material composition. P loss certainly depends on current landuse as well, but we do not include landuse here our focus is on natural variability in soil P status. There are only limited data that constrain the variation of L with these factors. Those data that do exist suggest that L varies non-linearly with climate—where mean annual precipitation (MAP) exceeds evapotranspiration (PEt), rates of loss appear relatively constant and almost an order of magnitude higher than in drier settings with annual negative water balances (Chadwick et al. 2003; Porder et al. 2007). For P specifically, active cycling by plants slow the rate of loss dramatically where MAP > PEt (Porder and Chadwick 2009). Thus we restrict the our analyses to regions with positive water balance, conservatively masking out areas for which (MAP − PEt) < −500 (Hilley and Porder 2008).

The hypothesis that latitudinal differences in the P status of ecosystems results from variation in the total amount of time soil material has been subjected to weathering explicitly subordinates variation in L to variation in t_b. To test this hypothesis, we derive a single value of L from both a chronosequence and deeply weathered outcrop from the humid montane tropical forests of the Hawaiian Islands (see Model Parameterization), and apply it to humid regions of the globe to see if latitudinal trends in predicted total soil P emerge that may plausibly explain the observed differences in ecosystem P status.

We further assume that the weathering zone, soil, and denudation rate have reached a steady-state condition ($\varepsilon_w = \varepsilon$). While any individual place within a landscape may not have steady-state weathering zone thickness (due to tree falls, landslides, etc.) there is evidence that many landscapes tend toward a steady state where weathering zone thickness remains constant over time (Hilley et al. 2010). In the steady state formulation, the mean weathering time of bedrock-derived material in the soil is:

$$t_b = \frac{\int_{Z-Z_s}^{Z} \frac{Z}{\varepsilon} dz}{Z_s} = \varepsilon^{-1}\left(Z - \frac{1}{2}Z_s\right) \quad (1)$$

By prescribing the initial concentration of a particular element of interest (in this case P, denoted q_{oP}; mol m^{-3}), and its loss rate due to chemical leaching (L_P; mol m^{-3} kyr^{-1}), we can write the concentration of P in the soil that is derived from the bedrock substrate (q_{bp}; mol m^{-3}) as:

$$q_{bP} = q_{oP} - L_P t_b = q_{oP} - \frac{L_P}{\varepsilon}\left(Z - \frac{1}{2}Z_s\right) \quad (2)$$

The other potential source for soil P is dust, whose residence time in the soil may be different than bedrock-derived material. This time depends only on the depth to which dust is incorporated into the soil (assumed here equal to Z_s) and ε (Okin et al. 2004; Porder et al. 2007), assuming that the soil/saprolite interface lowers in proportion to ε. This mean dust residence time is:

$$t_d = \frac{Z_s}{2\varepsilon} \quad (3)$$

The amount of P brought into the soil exogenously as dust is a function of the flux of dust (F_d; m kyr^{-1}), the concentration of P in that dust (q_{dP}; mol m^{-3}), and the fraction of dust incorporated into the soil rather than being eroded away (r). This fraction likely depends on a myriad of factors, including the extent of bioturbation, the depletion of the soils by weathering, local surface runoff, and the aerodynamic roughness of the surface. Currently, there is no framework from which to predict its value, which can range from 0 to 1. If dust is continuously mixed into the soil while it is denuded, the mean concentration of P delivered to the soil (q_{odP}) by dust deposition is:

$$q_{odP} = \frac{rF_d q_{dP}}{Z_s} t_d = \frac{rF_d q_{dP}}{2\varepsilon} \quad (4)$$

As with the bedrock-derived P, dust-derived P also is leached from the soil over time. In our model, P in the upper soil is subject to the same rate of loss as in the saprolite, though this may overestimate loss rates by discounting the role of plants in retaining nutrients (Jobbágy and Jackson 2004; Porder and Chadwick 2009). With this in mind, the concentration of dust-derived P in the soil after leaching (q_{dP}) is:

$$q_{dP} = \frac{rF_d q_{dP}}{2\varepsilon} - L_P t_d = \frac{rF_d q_{dP}}{2\varepsilon} - \frac{L_P Z_s}{2\varepsilon} \quad (5)$$

Finally, the total soil P concentration in the soil (q_{soilP}) is the sum of these two components:

$$q_{soilP} = q_o + \frac{rF_d q_{dP}}{2\varepsilon} - \frac{L_P Z}{\varepsilon} \quad (6)$$

Because q_{soilP} is contingent upon the initial P concentration of both parent material and dust, and parent material values in particular are highly variable with rock type (Taylor and McClennan 1985), we normalize the soil P concentration to the parent material concentration and report Q, the fraction of the parent material P concentration observed in the soil:

$$Q = \frac{q_{soilP}}{q_{oP}} = 1 + \frac{rF_d}{2\varepsilon}\frac{q_{dP}}{q_{oP}} - \frac{L_P}{q_{oP}}\frac{Z}{\varepsilon} \quad (7)$$

In this nondimensional form, the fraction of P relative to bedrock is simply a function of two parameters: a dimensionless dust contribution (δ) and a dimensionless leaching parameter (λ):

$$Q = 1 + \delta - \varepsilon \quad (8a)$$

Where

$$\delta = \frac{rF_d}{2\varepsilon}\frac{q_{dP}}{q_{oP}} \quad (8b)$$

And

$$\lambda = \frac{L_P}{q_{oP}}\frac{Z}{\varepsilon} \quad (8c)$$

Model parameterization

Calculation of Q requires estimates of r, F_d, ε, q_{dP}/q_{oP}, L_P/q_{oP}, and Z. We calculate denudation rates (ε) based on topographic relief (Hilley and Porder 2008) and note that such an approach is supported by data from low temperature thermochronology (Montgomery and Brandon 2002). While soil development can occur on shorter timescales than captured by such geologic proxies (Almond et al. 2007), our model attempts only to capture regional-scale variation over which average soil residence times are likely to be more strongly coupled to landscape development. We have fewer constraints on the relationship between ε and Z, and explore four end members here (Fig. 2). First, we follow Hilley and Porder (2008), and assume the relationship between weathering zone thickness and erosion rate is logarithmic, with thin weathering zones (0.5 m) at high erosion rates (2 mm yr^{-1}), and thicker weathering zones at very low erosion rates (Hilley and Porder 2008). Here we present results from two end members, one where weathering zones are $\sim$20 m at 10^{-6} mm/yr erosion rates (Shallow Exponential—SE), and one where weathering zones are assumed to be $\sim$100 m thick at that erosion rate (Deep Exponential—DE). Both exponential formulations, however, result in weathering zones that exceed local topographic relief at very low erosion rates (<10^{-3} mm yr^{-1}). It is unclear what mechanism would drive weathering deep below base level (Hilley et al. 2010), and thus we consider two additional scenarios (hereafter "relief-limited, RL") where weathering zone thickness is derived from the exponential relationship at high (>10^{-1}mm yr^{-1}) erosion rates, but at lower erosion rates weathering zone thickness is a linear function of erosion, and is limited by the total topographic relief in the region. This results in thin weathering zones in regions where there is very low erosion rate and topographic relief (Fig. 2).

We derive F_d using dust deposition rates from NCAR's CCSM-3 GCM (Mahowald et al. 2006), and assume the concentration of P in dust is the same as in average continental crust (Taylor and McClennan 1985). While there is evidence to suggest that P in dust is elevated ($\sim$100 mol m^{-3}) relative to continental crust (67 mol m^{-3}) (Lawrence and Neff, 2009), it is not known whether this elevation is a result of human activity, and we make the conservative assumption that dust has the same P composition as continental crust, which will reduce the importance of dust as a P source but is consistent with previous efforts to estimate the global influence of dust on soil

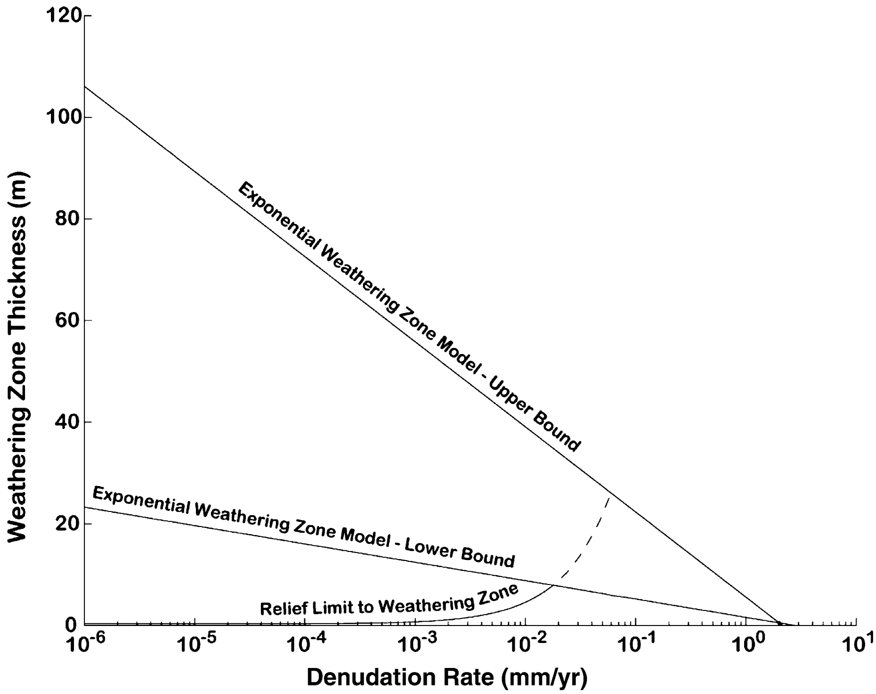

Fig. 2 The relationship between denudation rate and weathering zone thickness for the different scenarios used in this model. Deep and shallow exponential weathering zone scenarios (DE and SE in text) are calibrated by the few areas where cosmogenically derived denudation rates and weathering zone thickness have been reported. Relief limitation scenarios (RLDE and RLSE in text) assumes deep or shallow exponential fits hold at high denudation rates, but at lower rates the weathering zone thickness is limited by topographic relief (indicated by the *dashed line*). Derivation of these relationships from (Hilley and Porder 2008; Hilley et al., 2010)

P (Okin et al. 2004). In the same way, the fraction of dust that is incorporated into the soil (r) weights the relative effects of dust on P residence times. There is little data to constrain r in humid environments, and we allow this parameter to vary between 0 (no dust incorporation) and 1 (100% dust incorporation). We allow dust to be mixed to the depth of the soil, not into the saprolite, although some data from Hawai'i suggest that most dust is incorporated only into the upper 30 cm of soil (Kurtz et al. 2001).

Finally, the loss of P during residence in the saprolite and soil is also poorly constrained. Measurements of total P and comparison to immobile elements (Kurtz et al. 2000) allow quantification of the parent material P lost from the upper 50 cm of soil along a humid tropical montane chronosequence in Hawaii ($\sim$0.05 mol P m^{-3} kyr^{-1} at MAT 16°C, MAP 2,500 mm yr^{-1}; Vitousek 2004). Given the $\sim$200 mol m^{-3} parent material concentration of these flows, L_P/q_{oP} from this chronosequence is $\sim 2.5 \times 10^{-4}$ kyr^{-1}. Near the oldest site on this chronosequence we sampled an $\sim$80-m-deep transect through the weathering zone topped by a 4.1 ma basaltic flow. Assuming that the chemical weathering front propagates downward into fresh bedrock at a rate of 0.02 m/kyr as has been inferred elsewhere (Drever and Clow 1995), we calculate a similar L_P/q_{oP} along this depth profile. Combining the two datasets, assuming $q_{oP} = 200$ mol m^{-3}, yields an $L_P/q_{oP} \sim 2.9 \times 10^{-4}$ kyr^{-1} (Fig. 3). Note that we are only concerned here with climates with positive water balance, and assume the propagation rate is not sensitive to climatic variation within this already wet climate envelope. This is almost certainly not correct when the vadose zone extends to great depth (e.g., Lebedeva et al., 2010), but may be reasonable in cases where the extent of weathering is limited by the location of the shallow groundwater table (e.g., Hilley et al. 2010).

P losses may be particularly important in deep profiles because they can occur well below the rooting zone of plants, and thus proceed unimpeded

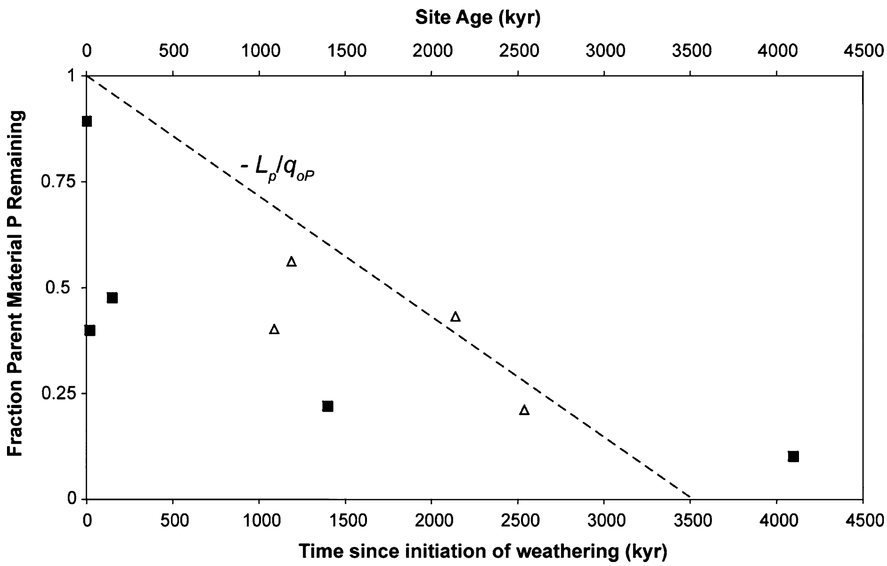

Fig. 3 Parent material P remaining in the upper 50 cm of soil from a 4.1 ma chronosequence in the Hawaiian Islands (*black squares*; data from Vitousek 2004) and in a deeply weathered profile at the 4.1 ma site (*open triangles*). Time since the initiation of weathering for the deep profile was calculated assuming a 4,100 kyr surface and a propagation of the weathering front of 0.02 m kyr^{-1} (Drever and Crow 1996). These data were combined to estimate a P loss rate, L_P/q_{oP}, of 2.9×10^{-4} kyr^{-1} by estimating a best fit line through the data but forcing the line through 100% P remaining at time = zero

by plant demand that can considerably slow P losses (Porder and Chadwick 2009). In the deep profile in Hawaii, P losses occur to at least 60 m depth, and on the granodiorite bedrock the Luquillo Mountains of Puerto Rico, there is a 50% reduction of P at the rock-saprolite boundary at ~8 m depth (Pett-Ridge 2009), both likely well beneath the rooting zone of plants. Thus in extremely thick weathering zones formed in humid environments, bedrock-derived P may be almost completely lost via leaching before it arrives at the soil. As a result variations in leaching rate may be important in driving differences in P status, but we apply a constant value of L_P/q_{oP}. to test the original hypothesis that the duration of weathering, rather than factors that affect leaching rate, results in latitudinal gradients in P status.

Caveats

We parameterized our model with the available data, but in many cases these are few and far between. The relationship between weathering zone thickness and erosion rate is highly uncertain, and plays a strong role in driving P loss predictions for any given location, as noted below. It is also important to note that our model is parameterized in terms of denudation rates, and thus depositional settings are not encapsulated in its results. This is problematic, particularly for large regions in Amazonia dominated by Oxisols that are hypothesized to be depositional (Buol and Eswaran 2000). If the depositional event occurred long enough ago that denudation rates have adjusted to the local topography, our model may be relevant in these settings, but as formulated it is explicitly intended only for denuding landscapes where the soils are created from the underlying parent material.

In addition, our assumption that denudation rate and weathering zone thickness are, on average, fairly tightly linked, is one that bears more consideration. While it is likely true on geologic timescales, and averaged over large regions, any examination of a series of tightly spaced road cuts will yield substantial variation in weathering zone thickness at much shorter spatial scales than the 0.5° pixels we consider in this model. We suspect this sub-pixel variation is likely the result of geologic and hydrologic variation, and may play an important role in driving the P content of a particular patch of soil. As further data provide a better understanding of the factors that control such local variation, such effects can be incorporated to improve local predictions of total P in soils. Nevertheless, if such local-scale heterogeneity is the primary driver of P status, it argues against large latitudinal gradients caused by differences in soil age.

Results

The effect of weathering zone thickness

We first consider scenarios where $r = 0$, i.e. no dust is incorporated into soil and the amount of P in soil is solely a function of the residence time of the rock-derived fraction and the leaching rate. In these scenarios, assumptions about the form of the denudation/weathering zone thickness function play a dominant role in determining our predictions of spatial variation in P status (Fig. 4). If weathering zone thickness is limited by relief (either in the Deep or Shallow scenario), even intracratonic regions that are denudation relatively slowly are likely to retain the majority of their rock-derived P (Fig. 4), and Q is similar between temperate (those unglaciated at the LGM) and tropical regions (median > 0.85, Table 1). The "Shallow Exponential" scenario produces similarly small P losses. However, in the Deep Exponential scenario, rock-derived P losses are considerably greater, and mean Q in the temperate and tropical zones are 0.59 and 0.31, respectively. There is also a distinct trend towards greater P losses at the equator as well as at ~30°S (driven by the low relief landscape in the Pampas of Argentina).

The effect of dust inputs

The addition of dust has a rejuventating effect on soil P across all scenarios, but does not substantially alter the trends explored in the "no dust" Scenarios (Fig. 5). The effect of dust is not directly proportional to its flux, since the calculated P soil is a concentration weighted average of the rock and dust derived P fluxes, the maximum dust influence on Q comes either where dust fluxes are very high (e.g. the Argentinian Pampas) or where the flux from rock is quite low (e.g. sub-Saharan Africa). Not surprisingly, the highest dust effects come when these two are combined. For example, in the Deep Weathering

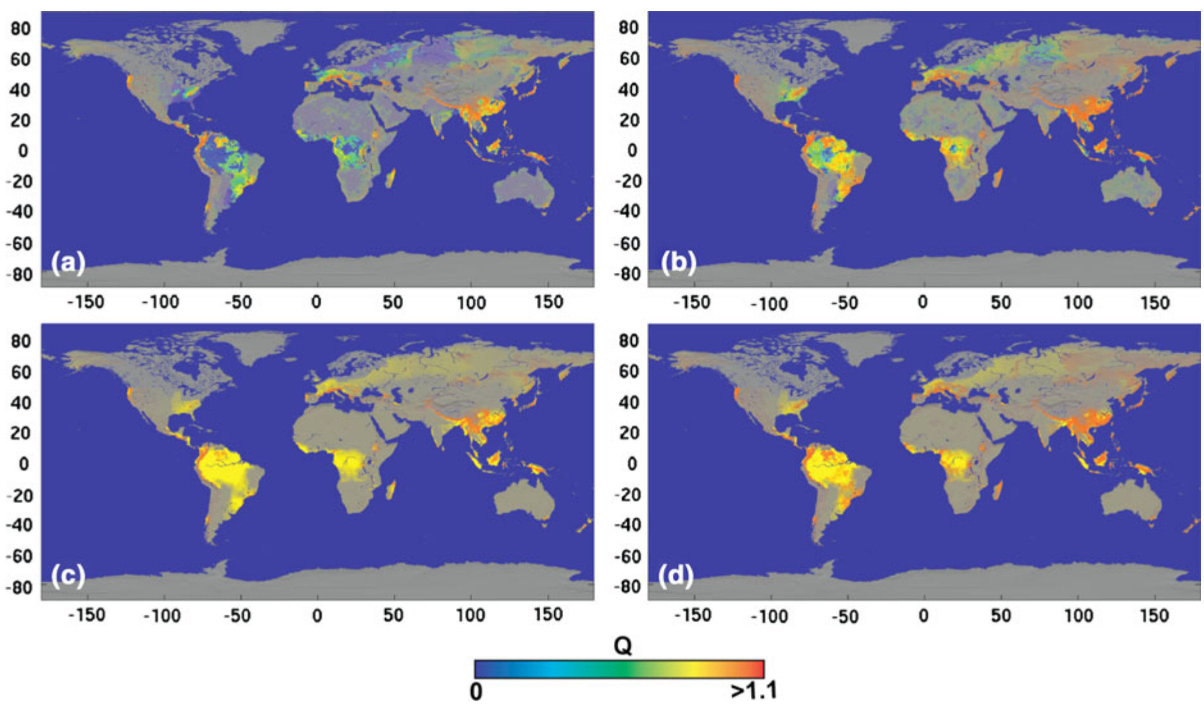

Fig. 4 The distribution of Q (soil P/bedrock P) for bedrock-derived P with no dust incorporated into the soil for the **a** DE, **b** SE, **c** RLDE and **d** RLSE. Scenarios defined in the text. The figure shows full color in regions where MAP − PEt > −500 mm yr^{-1}, and is increasingly transparent as water balance gets more negative below this threshold. Pixels that we covered in ice during the Last Glacial Maximum are also shown as grey

Table 1 The mean, median, standard deviation and quartiles of Q ($[P_{soil}]/[P_{bedrock}]$) in the temperate (those portions that were ice-free during the last glacial maximum) and tropical zones across the different weathering zone and soil scenarios

Scenario	Mean	Median	Std	25%	75%
Temperate zone ($N = 36137$)					
No dust flux					
RLDE	0.88	0.85	0.04	0.85	0.90
RLSE	0.91	0.91	0.06	0.85	0.98
DE	0.49	0.59	0.40	0.00	0.90
SE	0.77	0.91	0.31	0.70	0.98
Current dust flux					
RLDE	1.1	0.89	26	0.86	0.95
RLSE	1.2	0.96	26	0.89	0.99
DE	0.5	0.61	0.40	0.00	0.90
SE	0.8	0.93	0.35	0.75	0.98
LGM dust flux					
RLDE	2.1	0.94	150	0.86	1.0
RLSE	2.1	0.99	150	0.93	1.0
DE	0.61	0.68	1.2	0.00	0.93
SE	0.98	0.97	1.6	0.83	1.0
Tropical zone ($N = 18413$)					
No dust flux					
RLDE	0.87	0.85	0.04	0.85	0.85
RLSE	0.90	0.85	0.05	0.85	0.95
DE	0.38	0.31	0.38	0.00	0.77
SE	0.70	0.84	0.33	0.56	0.95
Current dust flux					
RLDE	0.98	0.87	0.74	0.86	0.95
RLSE	1.0	0.93	0.74	0.87	0.99
DE	0.40	0.35	0.38	0.00	0.78
SE	0.75	0.89	0.40	0.64	0.97
LGM dust flux					
RLDE	1.0	0.88	1.1	0.86	0.96
RLSE	1.1	0.93	1.1	0.87	0.99
DE	0.40	0.36	0.39	0.00	0.78
SE	0.77	0.90	0.41	0.65	0.98

RLDE relief-limited deep exponential, *RLSE* relief-limited shallow exponential, *DE* deep exponential, *SE* shallow exponential

Scenario the input of LGM rates of dust shifts the median Q in Africa from 0.16 to 0.28, whereas modern and LGM dust fluxes produce median Q in South America of 0.44 and 0.49, respectively. By far the largest changes in Q due to dust occur between 20° and 40°S, with the Pampas again driving the trend.

Dust fluxes have varied globally by a factor of ~3–4 over recent glacial-interglacial cycles (Rea 1994), and not surprisingly LGM dust fluxes have a slightly greater rejuvenating effect than do current fluxes (Fig. 5). Nevertheless, even LGM fluxes do not produce a dramatic gradient in P losses between the temperate and tropical zones. Thus while some sites are clearly strongly affected by dust inputs (Kurtz et al. 2001; Muhs and Budahn 2007; Pett-Ridge 2009), these inputs do not appear sufficient to drive large latitudinal gradients in P losses between the unglaciated temperate and tropical regions.

The effect of P loss rate

The loss of P from the weathering zone, before it ever enters the soil, may play an important role in determining the P status of ecosystems. Unfortunately, this loss rate is poorly constrained across rock type and climate. Our loss rates, calibrated on basaltic parent material (200 mol m^{-3} P) receiving 2,500 mm yr^{-1} rainfall, suggest that P depletion from parent material reaches near completion after about 4 million years. Thus if the advection time of rock-derived material before it reaches the soil exceeds that, the rock-flux is minor relative to that of dust derived material. However, data from other humid chronosequences on granitic substrate, particularly the Franz Joseph Chronosequence in New Zealand (MAT ~ 10°C, MAP 3000–6000 mm yr^{-1}, (Stevens 1968; Richardson et al. 2004), suggest that loss rates may be considerably (possibly 10x) faster on granites than on basalts (Stevens 1968). We explore sensitivity to this parameter by increasing L_p/q_{oP} by a factor of ten. While this has little effect on latitudinal trends, it has a dramatic effect on our prediction of Q in almost every location. High L_p/q_{oP} results in a prediction that most of the world is predicted to have soil that has almost no P relative to parent material, and thus there is no latitudinal trend in Q because it is close to 0 almost everywhere (Fig. 6). We suspect this loss rate is unrealistic, because average granitic parent material has ~700 ppm P (Taylor and McClennan 1985), and soils with less than 100 ppm P are rare (S. Porder, Unpublished data).

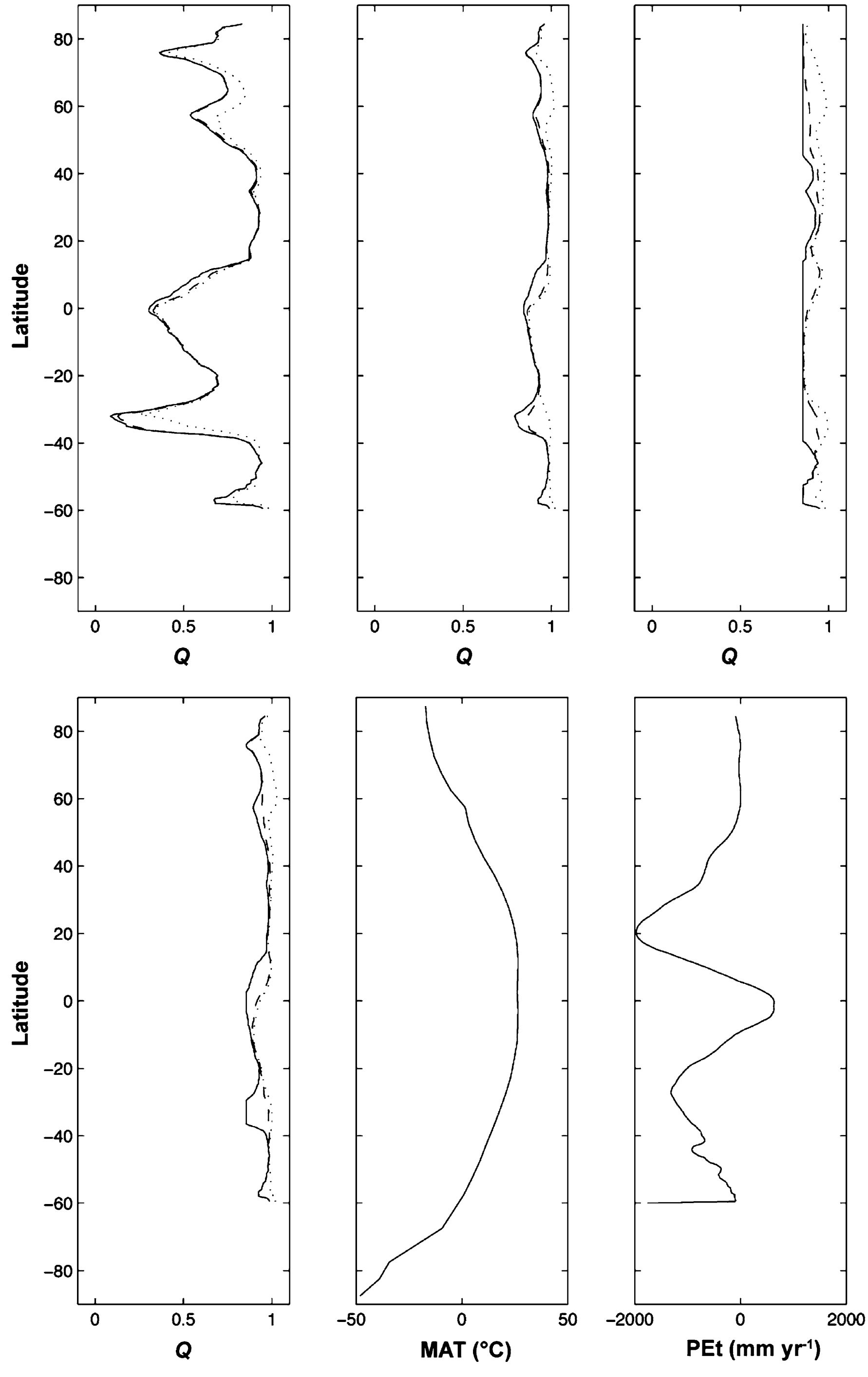

Fig. 5 Median values of Q plotted by latitude for $r = 0$ (solid), 1 (current dust flux; dashed line) and 1 (LGM dust flux; dotted line) for the four scenarios discussed in the text. **a** DE, **b** SE, **c** RLDE, **d** RLSE, **e** mean annual temperature, **f** potential evapotranspiration

Discussion

While P losses relative to parent material vary considerably across weathering zone and soil thickness scenarios, Q hardly varies between temperate and tropical latitudes, except in the Deep Exponential Scenario where it varies by less than a factor of two. Given a substantial body of literature that describes broad latitudinal differences in foliar nutrients (Vitousek 1984; Reich and Oleksyn 2004) and nutrient

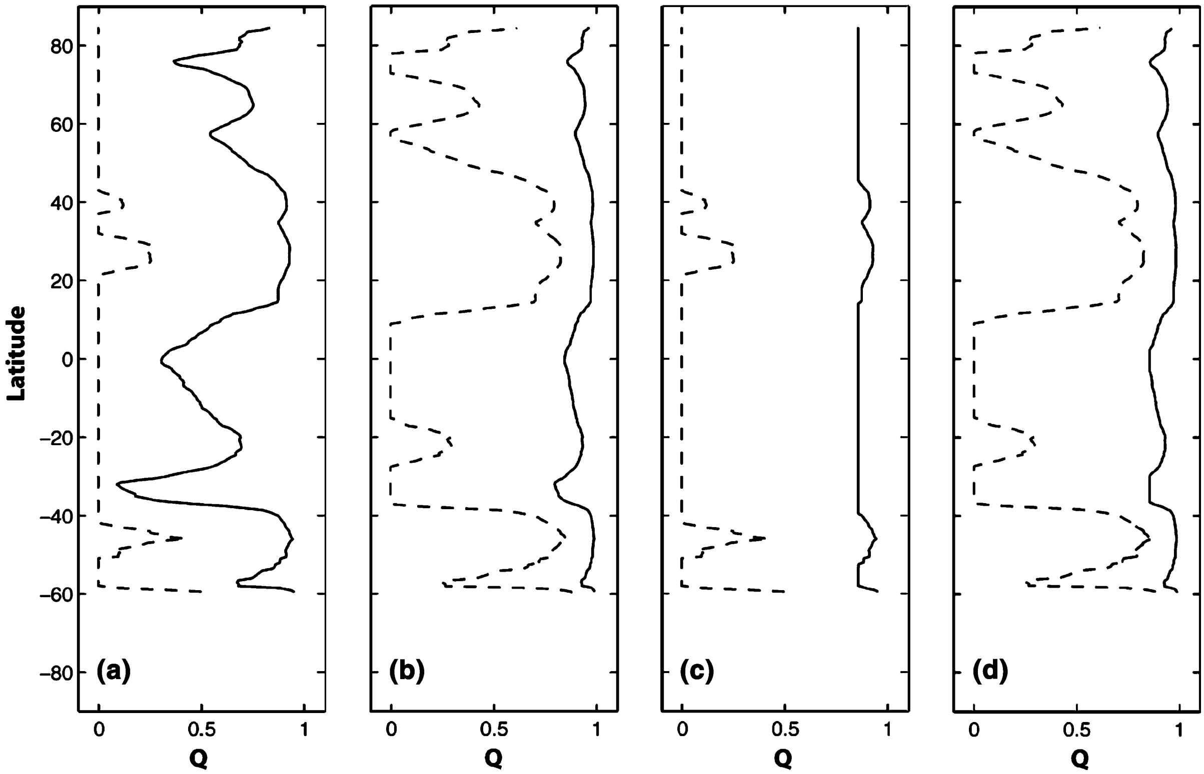

Fig. 6 The effect of variation in P loss rate (L) on the latitudinal distribution of Q assuming no dust inputs for **a** DE, **b** SE, **c** RLDE and **d** RLSE. Solid lines are for L_p/q_{oP} loss rates from Fig. 5, dashed lines are L_p/q_{oP} assuming 10× faster P loss

resorption (Yuan and Chen 2009), we must ask whether such subtle differences in P loss might be sufficient to drive these well documented patterns. In a basic sense, if the expected latitudinal gradients in substrate age are insufficient to explain the large inferred differences in P status and by extension total P, then one of two explanations must be invoked: (1) the loss rate must strongly covary with latitude and/or (2) total soil P is not a useful proxy for the amount of P cycling in ecosystems.

In our study, we calibrated L_p/q_{oP} based on a humid basaltic chronosequence in Hawaii. However, results from other chronosequences on the Island of Hawaii show that climate may exert a profound control on L_p/q_{oP}. In fact, soils that are ~350 kyr show little loss of P when the water balance is negative, while slightly wetter sites show substantial losses (Porder and Chadwick 2009), indicating that in this system, variations in L_P/q_{oP} may exert a far stronger control on P loss than substrate age. The ability of soil to retain P is also strongly dependent on redox conditions, which are linked to differences in water balance (Thompson et al. 2006). As such, it is plausible that the humid tropics have greater L_p/q_{oP} than humid temperate zones because of the generally higher rainfall and more positive water balances, and so systematic variations in climate might play a strong, if not dominant, role in controlling latitudinal gradients in soil P.

The composition and nature of parent material also may play a large role in determining soil P status through the abundance of P in rocks prior to chemical weathering, the degree to which geologic processes have created permeable paths in the bedrock, and the hydrochemical development of the saprolite as it weathers. P concentrations in rocks vary from a few to a few thousand ppm due to the presence or absence of trace mineral phases whose abundance is not easily predicted from mapped lithology (Taylor and McClennan 1985). For example, the South African Fynbos region sits atop extremely P poor sandstones, where precipitation is too low for leaching of this depleted parent material. In this case, dust supplies a substantial fraction of P found in soil (Soderberg and

Compton 2007). The degree to which rock is fractured may also allow deep penetration of meteoric fluids into rock that facilitate the conversion of bedrock to saprolite. In some cases without such pathways, weatherable rocks overlain by impermeable rocks may be unavailable for meteoric weathering, even in the case that the water balance is extremely positive. However, the presence of fractures in the rock may facilitate infiltration into the otherwise impermeable rocks, and facilitate weathering of the rocks below (Fetter 2000). Finally, the development of the permeability of the saprolite during pedogenesis likely plays an important role in soil P losses. As noted above, despite relatively similar climates, the greywacke-derived till that makes up the Franz Joseph chronosequence in New Zealand looses P almost ten times faster than Hawaiian basalts. The texture and mineralogy of Hawaiian rocks facilitates contraction of the soils as they weather; however, the perseverance of mineral phases such as quartz in granitic saprolites may allow high meteoric flow and weathering rates to be maintained to some depth below the surface. This may be why most of the P losses from the granodiorite that underlies the montane forests in Puerto Rico occur not in the soil but in the rock as it transitions to saprolite, well below the rooting depth of plants (Pett-Ridge 2009), while losses above the saprolite are negligible.

Finally, this approach considers soil and saprolite P to reflect the steady accumulation and leaching of P from near Earth's surface. However, there are data to suggest that P depletion in parts of the tropics may bear the imprint of the past geologic history of these areas. For example, laterization of Precambrian bedrock in the Carajás Mountains in the Brazilian Amazon started in the late Cretaeous, and sporadic weathering during fairly short intervals has been ongoing since that time (Vasconcelos et al. 1994). Some of these episodes may be related to climate changes in the late Miocene (Vasconcelos et al. 1992), while others may reflect baselevel and groundwater changes associated with tectonic events that allowed weathering to penetrate deep into the craton's substrate. Thus, the history of climate, uplift, erosion, and topographic and hydrologic baselevel may combine to create deep depleted parent material that can not supply substantial P to ecosystems no matter what the modern day soil residence time.

This work is focused on loss of total P relative to parent material, which changes dramatically over time across at least one well-studied chronosequence (Chadwick et al. 1999), more dramatically, in fact, than either "biologically available" or total soil P concentration (Crews et al. 1995). However, in some environments, P may be removed from the biologically available pool through the occlusion of P into physical and chemical aggregates that are difficult to biologically access, without losses of total P (Vitousek et al., in press). Because the availability of P to ecosystems may span a continuum from easily accessed to recalcitrant P (Syers et al. 2008), the discussion of P limitation is predicated on what pools are considered "biologically available" (Cross and Schlesinger 1995). Unfortunately, our understanding of what constitutes these pools is rudimenatary at best (Richter et al. 2006). The model presented here is designed to capture only variations in total P that arise from leaching over time, and so cannot address the hypothesis that latitudinal variations in P status arise from latitudinal changes in the rate at which P is transferred from "available" to "unavailable" pools. However, invoking such a rate difference would also require a rejection of the hypothesis that time, rather than differences in P transformation rate, drive latitudinal trends in P status.

This model is admittedly simplistic—the lack of data on how P leaching rate varies with climate and rock type, as well as information on what controls weathering zone thickness and thus soil residence time, precludes a more detailed formulation. However to date ours is the only attempt we know of to test a hypothesis that has held sway in the biogeochemical community for decades—that tropical soils are P depleted because they are *older* (in the sense of residing longer in the landscape) than temperate soils. Surprisingly, we find little support for this hypothesis. As an alternative working hypothesis, we suggest instead that systematic latitudinal changes in climate that affect leaching rate, the hydrochemistry of soil, and processes that transfer P between biologically available and recalcitrant pools appears to provide a more compelling explanation of observed trends than do systematic variations in substrate age.

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