

Interdependency of plants and animals in controlling the sodium balance of ecosystems and the impacts of global defaunation

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Sodium, an element which is needed by animals but often toxic in high concentrations to plants, may be deficient and limit animal abundance in inland continental regions, but may be overabundant and limit plant productivity in coastal regions. Here we present data from 50 independent plots (including leaf data from more than 2480 individual trees) showing that leaves in the Amazon basin uptake high amounts of sodium (Na) in a manner more similar to the essential cation potassium (K) than to the toxic cation aluminium (Al). Leaf Na increases linearly with soil Na concentrations, and there is no apparent mechanism for selective exclusion of Na in comparison to K, a key attribute of halophytes. This indicates that the Amazon basin is broadly non-halophytic and increased sodium concentrations in non-halophyte plants often decrease plant productivity. Total Na concentrations are ~ 10 times higher in coastal regions than inland regions. Such concentration gradients in nutrients may have been reduced in the past because large animals that were abundant in the Pleistocene have been hypothesized to play a large role in reducing nutrient concentration gradients at continental scales. We use a diffusion model and a Na loss rate based on empirical data to estimate that large animals may have moved significant quantities of Na inland away from coastal regions in the Amazon Basin. Therefore, our simple model suggests that large animals may play an important, yet diminishing, role in maintaining the sodium balance of the planet.

Of all elements, sodium plays a particularly intriguing double role in the terrestrial biosphere, as an essential nutrient for animal biology, but often a toxic one for plants. Nevertheless, land animals and plants must coexist, because animals ultimately depend on primary productivity to meet their energy requirements and most animals get their sodium input through eating plants. Thus, the interactions between plants, animals, and sodium is inherently more complex and potentially fraught than other nutrient dynamics. In tropical forests, sodium deficiency may limit invertebrate abundance in the continental interiors (Kaspari et al. 2008, 2009). In contrast, sodium toxicity is a major problem for plants in many parts of the world, especially in certain coastal or irrigated agricultural systems since evaporation removes the water but leaves the cations (Loomis and Conner 1992, Blumwald et al. 2000, Tester and Davenport 2003). Most sodium input to ecosystems is through sea salt aerosols that decrease exponentially from the ocean (Stallard and Edmond 1981) through limited mineral inputs from highly saline soils; or through river systems (Gaillardet et al. 1999). In essence, sodium is not evenly distributed across the planet, leading to large sodium concentration gradients in ecosystems, at scales ranging from meters to continents.

Sodium is not considered an essential nutrient for plants (although it may be beneficial in low concentrations to

some plants (Marschner 1995)), and indeed is most often detrimental in high quantities. In animals, sodium pumps maintain gradients of cell concentrations and membrane electrochemical potential, but in plants this function is generally performed by K, not Na. In fact, the presence of Na in soils generally impedes plant growth by a number of mechanisms, such as by impeding the flow of water by dispersing clay minerals; imposing a chemical ‘drought’ by lowering the water potential of soils; and accumulating around the root cambium and interfering with the plants’ ion uptake (Grattan and Grieve 1992). Although Na is not needed by plants as an essential nutrient, it is passively accumulated because the negative electric potential difference at the plasma membrane and low cytosolic Na concentrations strongly favor the movement of Na into cells. Sodium is energetically expensive to expel since Na ions have to be transported against their electrochemical potential (Blumwald et al. 2000). In rapidly transpiring plants typical of tropical forests (Fisher et al. 2009), transport into the xylem of plants is likely a passive process (Tester and Davenport 2003). Once in the leaves, Na is pushed into vacuoles, where it accumulates to avert the deleterious effects of Na in the cytosol (Marschner 1995).

Salinity is generally thought to be the limiting nutrient for animals in the western Amazon because it is distant from

its main source of sea salt aerosols. A recent group of studies has found that when inland tropical forests are fertilized by salt, the salt is quickly accumulated into the litter layer and consumed by invertebrates (Kaspari et al. 2008, 2009). They found that salt fertilization increased the abundance of termites seven-fold, and predatory ants two-fold, indicating that the effects of sodium could cascade up and down through the food web and it was Na, and not Cl, that was in fact the limiting nutrient. Other tropical areas have been shown to be Na-limited for invertebrates (Kaspari et al. 2009) and also for larger animals such as elephants (Weir 1972). High latitude ecosystems are also Na-limited for a variety of species including moose (Botkin et al. 1973), deer (Weeks and Kirkpatrick 1976) and squirrels (Weeks and Kirkpatrick 1978). Abiotic factors have long been recognized to generate steep Na gradients through the deposition of oceanic aerosols. Work back to Blair-West has shown fitness consequences for animals, such as reduced lactation by rabbits in salt limited regions as a consequence of such a gradient in Na (Blair-West et al. 1968).

A recent but rapidly growing literature supports the general notion of large animals playing important ecological roles in nature (Terborgh and Estes 2010). Recent work has argued that over long timescales, mammalian herbivores can flatten sharp concentration gradients of elements through the fundamental processes of feeding, moving, defecating and urinating (Stevenson and Guzman-Caro 2010, Abbas et al. 2012). Animals are well known to move various nutrients around within and among ecosystems over smaller scales of space and time. Seabirds, for example, are important vectors of nitrogen from sea to land, and thus have major impacts on terrestrial plant communities (Croll et al. 2005, Maron et al. 2006, Young et al. 2010). Air-breathing marine mammals and birds bring nitrogenous nutrients and elemental iron from deep water to the euphotic zone, thus increasing production (Lavery et al. 2010, Roman and McCarthy 2010). In preindustrial human societies salt was a limiting commodity and early human societies spread it long distances before modern transportation (Kurlansky 2003).

While the behavioral and nutritional ecology underlying animal movement is complex, and differs distinctly among different species, there are some useful analyses of nutrient biogeochemistry that can be considered if we make the simplifying assumption that individual daily displacements of animals are random in the context of millennial-scale biogeochemistry. In particular, by employing a random walk model of animal movement, we lose some of the ability to analyze specific species in defined landscapes, but we gain some traction to estimate the aggregate nutrient translocation by all animals in an ecosystem, over large spatial and temporal scales. Previous work has suggested that larger animals are disproportionally important for longer distance transport of nutrients, but that small microfauna may still play an important role of fine scale nutrient distribution (Doughty et al. 2013, Wolf et al. 2013).

The hypothesis that animals (especially large animals) have a substantial capacity to translocate nutrients raises questions about the importance of past and future defaunation on this ecosystem function (Doughty et al. 2013, Wolf et al. 2013, Dirzo et al. 2014). The world has been undergoing a gradual

defaunation since the Pleistocene. The first major wave of large animal extinctions occurred in the late Pleistocene, when ninety-seven genera of large animals (> 44 kg) were lost (Barnosky et al. 2004). South America was particularly affected by these extinctions with 64 large animal species (> 10 kg) going extinct (Lindsey and Barnosky 2008). Prior theoretical work showed that the capacity of mammalian herbivores to translocate nutrients over long distances hinges primarily on their day range and gut passage time, and secondarily on their metabolic demand and population size (Wolf et al. 2013). All of these factors are closely linked to body size (Damuth 1987, Carbone et al. 2005, de Magalhães and Costa 2009), which suggests that it is possible to estimate these physiological and behavioral aspects of animal ecology for species about which little is known aside from paleontological evidence. In the case of Amazonian megafauna, we estimated that the end-Pleistocene mass extinction may have effectively ‘turned off’ the potential for lateral nutrient flow in terrestrial Amazonia possibly partially explaining contemporary P limitation in the eastern Amazon (Doughty et al. 2013).

Here we report on sodium concentrations in leaves and soils across South America, with three aims. First, we use these data to look for indications of sodium stress in plants and to calculate an empirical sodium loss rate. We then create a map of leaf sodium concentrations in South America, and we examine the potential effects of large animals on sodium movement looking at the past defaunation in South America. Finally, we map global sodium sources, and compare this to lateral distribution capacity to estimate regions of sodium deficiency over the entire globe.

Material and methods

Data collection methodology

We compiled measurements of leaf and soil sodium concentrations from 50 independent sites (Supplementary material Appendix 1, Table A1, locations shown in Fig. 2d), based on the RAINFOR datasets of Patino and Quesada (Quesada et al. 2010, Patino et al. 2012), French Guiana (Baraloto et al. 2011, 2012, Fortunel et al. 2014) and Colombia (Golley et al. 1978) (each groups methods for analyzing the cations are briefly described in Supplementary material Appendix 1). We estimate wood sodium concentrations as a ratio of leaf concentrations based on 306 individual tree species from 5 sites from Furch and Klinge 1989, Supplementary material Appendix 1, Table A2). We sum soil, wood, and leaf concentrations to the plot level (kg km^{-2}) using measured plot woody biomass, leaf mass area, leaf area index and soil depth and structure where available.

Regions of high soil salinity were mapped using the FAO-UNESCO Soil Map of the World (FAO 2013) including salt flats, regions classified as the phase type sodic, and soil types classified as solonetz and soloncheks (generally corresponding to Mollisols and Alfisols with Natric horizons in US Soil Taxonomy). Sodium concentrations of the world’s major rivers were collected from Gaillardet et al. 1999 (Fig. 4b).

Modelling methodology

We model the concentrations of ecosystem sodium (Na kg km⁻²) using the following budget equation:

$$\frac{dNa}{dt} = \phi \frac{d^2 Na}{dx^2} - KNa + G \quad (1)$$

where K is a first order loss rate of sodium (Na) and G is a gain rate from sea salt aerosol deposition. We estimate G as the % of total SSA deposition to enter the foliage using the mean foliar sodium concentration (Table 1) and the steady state loss rate (Table 1) (0.0130 yr⁻¹ × 927 kg km⁻² = ~ 12 kg km⁻² yr⁻¹). We use a simple diffusion based model to predict animal nutrient distribution (Φ km² yr⁻¹) over long distances and timescales.

Ecosystem sodium input rates were estimated from soils, sea salt aerosols and rivers. We estimate the aerosol input rates by combining leaf Na concentrations with modelled and measured penetration of sea salt aerosols from Sofiev et al. 2011, their Fig. 11A (Stallard and Edmond 1981, Sofiev et al. 2011, Stallard 2012a, b). We estimate input at 8–15 µg SSA m⁻³ (Sofiev et al. 2011) near the coast of Colombia, which means a deposition of 6 ng cm⁻² h⁻¹ with an average wind speed of 3.4 m s⁻¹ (McDonald et al. 1982) for a total deposition of ~ 4000 kg Na km⁻² yr⁻¹. This is supported by estimates of atmospheric sodium inputs across the Amazon (assuming 2.5 m rain) at 4000 kg Na km⁻² yr⁻¹ near the coast. These numbers are in line with results from Puerto Rico (Stallard and Edmond 1981, Stallard 2012a, b).

To estimate the steady state loss rate (K) we use the following equation:

$$K = \frac{G}{Na} \quad (2)$$

where G is the gain rate and Na is the total ecosystem Na concentration. We estimate the total ecosystem Na concentration as sodium in the leaf biomass, the wood biomass, and the soils to soil depths as listed in Quesada et al. (2010). We assume that below 2 m there are few roots and the sodium is no longer accessible to the biota. To sum the leaf chemistry (mg g⁻¹) to the canopy scale (kg km⁻²), we use measured leaf area index (LAI) (m² m⁻²) and measured leaf mass area (LMA) (g m⁻²). To estimate the effect of megafauna herbivory on the loss rate we simulate the loss rate with and without herbivory.

Although movements of individual animals over subdaily timescales require detailed boundary conditions to model, the average movement of populations of animals over larger timescales can be usefully modelled as a diffusion process (Skellam 1951, Okubo and Levin 2001, Ovaskainen and Crone 2009). The lateral fluxes of populations, and the materials are then modelled using a partial differential equation, in which the diffusivity governing lateral flow is determined by the characteristics of the animal population. The net lateral flux will be largest in regions of stark nutrient concentration gradients such as river valleys. To estimate the diffusivity of nutrients based on body size and distribution, we make use of a large literature on scaling theory (West et al. 1997) describing the wide range of animal physiology and behaviour that is correlated with animal size, including day range (DD), metabolic rate (MR) and food passage time (PR). We calculate a diffusion term (Φ) for dung (see Doughty et al. 2013, Wolf et al. 2013 for complete derivation and explanation of terms) according to the following equation:

$$\Phi = (1 - \epsilon) \times MR \times \frac{PD}{\alpha B} \times \frac{(DD \times PR)^2}{2 \times PR} = \frac{0.78 \times 0.05 \times M^{1.17}}{\alpha B} \quad (3)$$

where M is animal body mass, MR is metabolic rate, DD is day range, PR is food passage rate, ϵ is fraction of consumed Na that is retained in body mass, B is plant biomass that is estimated as leaf mass per pixel, of which α is the edible fraction. We had previously calculated the overall mass-scaling coefficient for Φ to be 1.17 (ranged by ± 0.24 in a sensitivity study), which shows that large animals are disproportionately important in the spread of nutrients based on body mass (a coefficient of 1 represents proportional scaling with animal mass) (Doughty et al. 2013).

Animals typically lose sodium through urine, versus through dung for excretion of phosphorus. Nevertheless, elephants often drop dung and urinate together (Rees 1983), and synchronous defecation appears to be present in several species of ungulates, and such allelomimetic behaviour may have adaptive value in the wild (Scott 1969). We therefore, do not modify our scaling coefficients from a previous analysis of phosphorus translocation. However, we acknowledge that this coefficient may need some further refinement in

Table 1. Mean sodium concentrations for South America for coastal and inland regions. Data locations are coloured dots in Fig. 2. Coastal areas are defined as being within ~ 100 km of the coast. Errors are standard errors.

| | Mean leaf Na ¹ (kg km ⁻¹) | Mean wood Na ² (kg km ⁻¹) | Mean soil Na ³ (kg km ⁻¹) | Total Na ⁴ (kg km ⁻¹) | Estimated SSA input ⁵ (kg km ⁻¹) | Steady state loss rate yr ⁻¹ ⁶ |
|---------|---|---|---|---|--|---|
| Coastal | 927 ± 161 (n = 11) | 190 × 10 ³ | 118 × 10 ³ ± 26 × 10 ³ (n = 11) | 308 × 10 ³ | ~ 4000 kg km ⁻² yr ⁻¹ | 0.0130 yr ⁻¹ |
| Inland | 140 ± 7 (n = 39) | 23.7 × 10 ³ | 9 × 10 ³ ± 2.6 × 10 ³ (n = 39) | 33 × 10 ³ | 0 kg km ⁻² yr ⁻¹ | 0.0130 yr ⁻¹ |

¹Using measured LAI and measured LMA g m⁻².

²Estimated based on wood/leaf Na ratios of 3.68 ± 4.5 (SD) from Furch and Klinge (Supplementary material Appendix 1, Table A3, n = 264 tree species), and measured total woody biomass in Mg ha⁻¹.

³Estimated using soil depth and bulk density from Quesada et al. 2010.

⁴Soil + leaf + wood.

⁵Coastal sea salt aerosol input of at 8–15 µg SSA m⁻³ from Fig. 11a in Sofiev et al. 2011, deposition from Table 5 in McDonald et al. 1982 assuming mean wind speed of 3.4 m s⁻¹. Stallard and Edmond (1981) estimate of atmospheric sodium inputs across the Amazon (assuming 2.5 m rain) at 4000 kg Na km⁻² yr⁻¹, near the coast. These numbers are in line with results from Puerto Rico (Stallard and Edmond 1981, Stallard 2012a, b).

⁶Assume loss rate is the same for inland as the coast.

the future if it is determined that the allometric coefficients (especially the exponent) for the gut passage time, is different between urine and dung.

For the Amazon, we estimate that the diffusion coefficient is $4.4 \text{ km}^2 \text{ yr}^{-1}$ as the mean from a sensitivity study ($2.2\text{--}6.6 \text{ km}^2 \text{ yr}^{-1}$) following the methodology listed in Doughty et al. (2013). We estimate that both of these coefficients changed to modern values $\sim 12\,000 \text{ ybp}$ (Wolf et al. 2013).

We recognize the many potential uncertainties inherent in such an analysis and therefore, we have modelled the impact on sodium movement by animals under a wide range of possible scenarios in a detailed sensitivity study (Supplementary material Appendix 1, Table A3 and A4). We vary the following variables: mean wood to leaf sodium ratio, sea salt aerosol input, loss rate (K), megafauna present in the Amazon basin, animal body mass, and the diffusion coefficient ($4.4 \text{ km}^2 \text{ yr}^{-1}$).

Results

We aggregated leaf and soil sodium concentrations from 50 plots in the Amazon basin where both leaf and soil sodium data existed. To estimate leaf sodium stocks we combine measured leaf mass per area and leaf area index with leaf sodium concentrations, and found that coastal regions have leaf sodium stocks ~ 6.6 times higher than inland areas ($927 \pm 161 \text{ kg km}^{-2}$ in coastal areas vs 140 ± 7 in inland areas) (Table 1). Based on the literature, we estimate the mean wood to leaf sodium ratio (mg Na g^{-1} wood over mg Na g^{-1} leaf) is 3.68 ± 4.5 (SD) ($n = 264$ tree species, Supplementary material Appendix 1, Table A3) (Furch and Klinge 1989). However, this mean masks much variation – about half of the sites had a higher Na stock in the wood while the other half had a higher stock in the leaves and we explore the potential impact of this variation in a sensitivity study. Based on this ratio, and in situ measured woody biomass for each site, we estimate a mean wood sodium stock of $190 \times 10^3 \text{ kg km}^{-2}$ along the coast and $23.7 \times 10^3 \text{ kg km}^{-2}$ inland. We estimate average sodium stocks in the soils using the RAINFOR database for bulk density and soil depth at $118 \times 10^3 \pm 26 \times 10^3 \text{ kg km}^{-2}$ along the coast and $9 \times 10^3 \pm 2.6 \times 10^3 \text{ kg km}^{-2}$ inland (Supplementary material Appendix 1, Table A2). Combining leaf, soil and wood sodium stocks, we estimate a total mean sodium stock of $308 \times 10^3 \text{ kg km}^{-2}$ along the coast compared to $33 \times 10^3 \text{ kg km}^{-2}$ inland, an approximate 10 fold difference.

We compared uptake factors (ratio (unitless) of leaf concentration (g kg^{-1}) to soil concentration (g kg^{-1})) for the three cations: aluminium, potassium, and sodium (Supplementary material Appendix 1, Table A1) to determine whether sodium accumulated by plants is quantitatively more similar to a toxic element (aluminum) or an essential one (potassium). Aluminum concentrations in leaves are essentially identical to concentrations in soil (0.99 ± 0.24 , $n = 47$). By contrast, potassium is accumulated and concentrated in leaves (96 ± 12 , $n = 60$). By this metric, Na is quantitatively more similar to K as it is also highly concentrated in leaves (52 ± 7 , $n = 45$). This compares to average K and Na soil concentrations of $0.044 \pm 0.003 \text{ g mg}^{-1}$

($n = 54$) and $0.017 \pm 0.005 \text{ g mg}^{-1}$ ($n = 54$) respectively. This suggests that sodium is passively taken up along the electrochemical gradient with all the other cations and not actively excluded like aluminium. Sodium and potassium have a similar chemical charge (+1) and size (0.358 nm Na vs 0.331 nm K), and crop species are often classified based on their ability to substitute Na^+ with K^+ (for instance beets, turnip, and swiss chard can replace a high proportion of K^+ with Na whereas in maize, bean, and lettuce no substitution of K^+ is possible) (Marschner 1995).

In our sites, leaf sodium increases approximately linearly ($p < 0.001$) with increased soil sodium (Fig. 1 top). Likewise, the ratio of potassium to sodium declines approximately linearly ($p < 0.001$) with increased soil sodium (Fig. 1 middle). The ratio of uptake (leaf/soil K to Na ratio) shows no significant variation ($p > 0.05$) with soil sodium, suggesting that in these communities, species on average do not possess the means to exclude sodium from leaves at high soil sodium concentrations, as is characteristic of halophytic (salt loving) species.

We can estimate a mean residence time of sodium in the biota (assuming that coastal ecosystems are in steady state) if we know both the sodium input from sea salt aerosols and the total concentration of sodium in the biosphere (leaves, wood, and soil to $\sim 2 \text{ m}$). We estimate sodium input along the coast at $\sim 4000 \text{ kg km}^{-2} \text{ yr}^{-1}$ (Table 1). We estimate total coastal sodium concentration ($308 \times 10^3 \text{ kg km}^{-2}$) which allows us to calculate a simple steady state loss rate [Eq. 2] of $\sim 0.0130 \text{ yr}^{-1}$. We ran our model with a lateral diffusion coefficient for herbivores of $\sim 4.4 \text{ km}^2 \text{ yr}^{-1}$ (calculated in previous work (Doughty et al. 2013) which includes

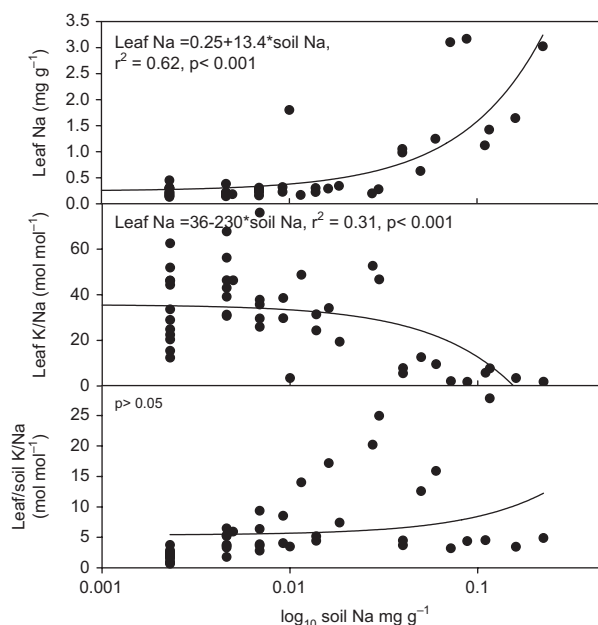


Figure 1. Leaf sodium and potassium concentrations versus soil sodium concentrations – (top) leaf sodium concentration (mg g^{-1} , $n = 50$), (middle) leaf potassium over sodium concentration (mol mol^{-1} , $n = 50$), and (bottom) leaf K/Na divided by soil K/Na (mol mol^{-1} , $n = 45$) compared to \log_{10} soil concentration ratios (mg g^{-1}). There are significant linear relationships for the top and middle figures ($p < 0.001$), but not for the bottom figure ($p > 0.05$).

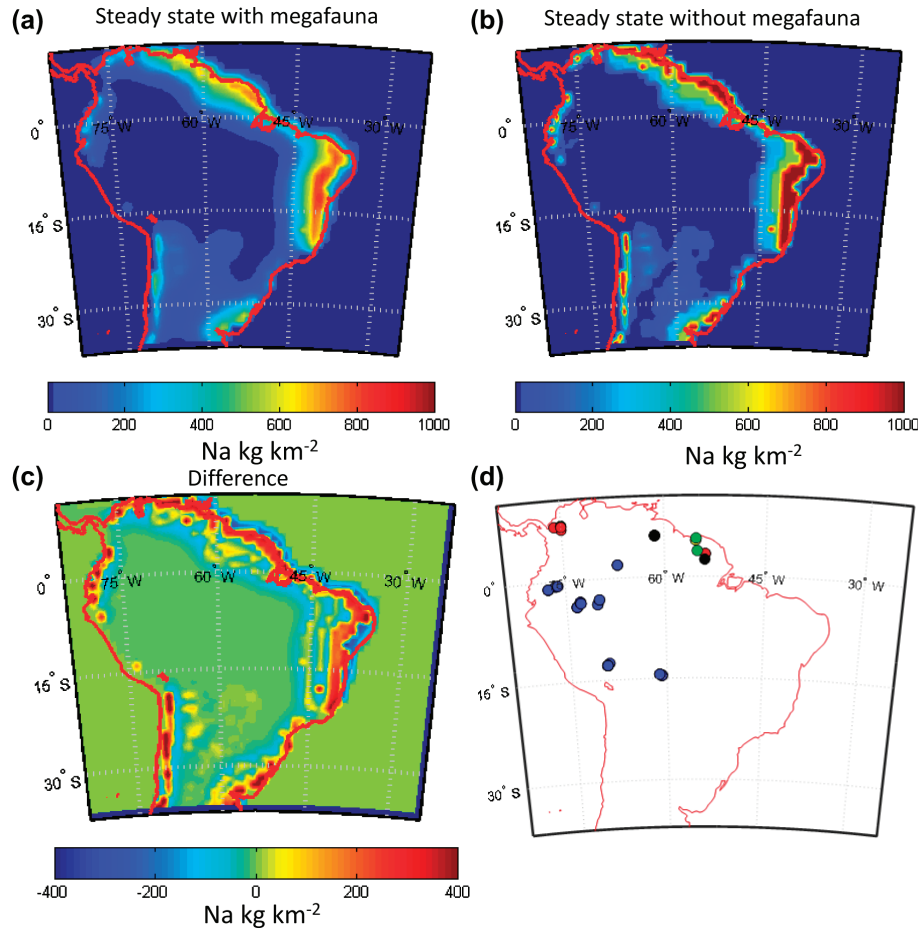


Figure 2. Modelled estimate of sodium distribution. (a) Estimated movement of sodium by herbivores for steady state in South America prior to extinctions (~15 000 ybp), (b) steady state, and (c) the difference between the steady state with megafauna and without. (d) Circles in South America are measured leaf sodium concentrations with red $> 1000 \text{ kg km}^{-2}$, yellow > 750 and $< 1000 \text{ kg km}^{-2}$, green > 500 and $< 750 \text{ kg km}^{-2}$, black > 250 and $< 500 \text{ kg km}^{-2}$, and blue $< 250 \text{ kg km}^{-2}$.

the Pleistocene megafauna) and find much sodium is spread by herbivores to the inland regions indicating that herbivores may previously have made an important contribution to the loss rate (Fig. 2). For instance, our simulations suggest that without megafaunal transport of sodium, steady state sodium concentrations could have ~ doubled in some coastal regions and decreased to close to zero further inland relative to pre-extinction levels (Fig. 3).

We used Eq. 1 to simulate sodium concentrations in both South America before and after the Pleistocene extinctions (Fig. 2). Prior to extinctions, large animals may have played an important role distributing the sodium inland but this role was largely diminished following their extinctions (Fig. 3). Following megafauna extinctions total concentrations of sodium increase slightly in all of the Amazon Basin, but this is entirely due to the large build up along the coasts – the majority of regions lose sodium (Fig. 3).

Finally, we estimate sodium limitations globally. Sodium from sea salt aerosols provides sodium mainly to coastal regions within 100 km of the coast. Sodium in soils is fairly randomly distributed throughout the planet but more typical in drier desert conditions (Fig. 4a). Sodium concentrations in rivers are generally high in temperate and desert

areas but low in tropical and most boreal regions (Fig. 4c). Major tropical rivers such as the Amazon or the Congo have very low sodium content ($80 \mu\text{mol l}^{-1}$ and $96 \mu\text{mol l}^{-1}$), only 6–7% the concentrations found in other major world rivers (Gaillardet et al. 1999). There does not appear to be greater sodium within the river floodplains of the Amazon compared with the terra firme soils (Furch and Klinge 1989). Sodium inputs and concentrations appear to be lacking most conspicuously in the Amazon and Congo basins as well as in Siberia.

If we posit that sodium can be spread outside the main source regions depicted in Fig. 4 through the lateral transport by herbivores, it is important to map this diffusivity in relation to sodium gradients. Current herbivore lateral diffusion capability is greatest in Africa and southeast Asia where megafauna are still present or were present until recently (Fig. 4b). The green regions in Fig. 4d are the likely sodium limited places on the planet where there is neither an abiotic source of sodium nor many large herbivores to distribute this sodium (Fig. 4d). The most likely sodium limited regions, and those most dependent on salt licks (which we are unable to account for in our maps due to their small and disperse nature) are the Amazon basin and Siberia (Fig. 4d).

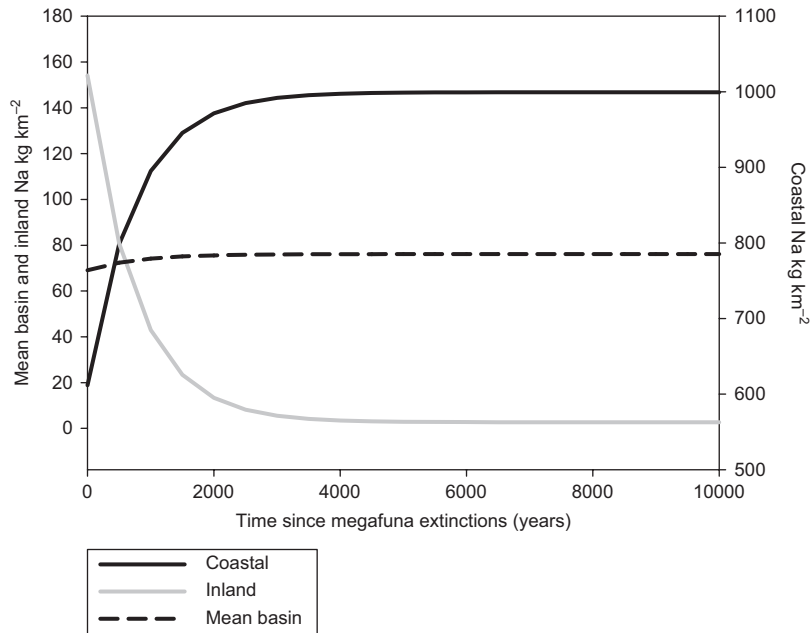


Figure 3. Changes in sodium concentrations over time. Estimate of Na concentrations over time in three locations, coastal (solid black), inland (grey line), and continental average (black dotted line) for South America. Time zero is the extinctions of the Pleistocene megafauna in South America.

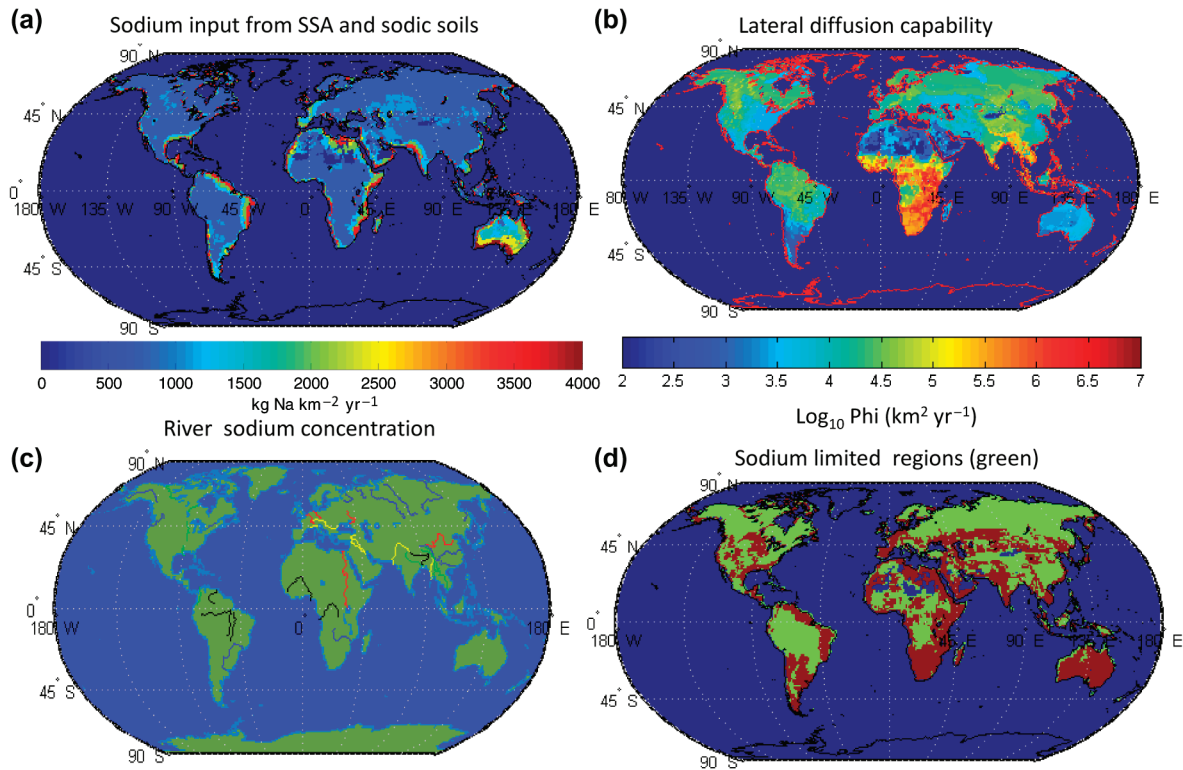


Figure 4. Global estimates of sodium limited regions. (a) A combination of modelled penetration of sea salt aerosols (Sofiev et al. 2011) onto land regions plus soil types that contain salt such as sodic soils, salt flats or saline soil types from the FAO soil map (FAO 2013). (b) An estimate of modern lateral diffusion capability based on animal size (see Wolf et al. 2013 for details). (c) Sodium in the major global rivers from Gaillardet et al. 1999 with black $< 100 \mu\text{mol l}^{-1}$ Na, blue $100\text{--}300 \mu\text{mol l}^{-1}$ Na, green $300\text{--}700 \mu\text{mol l}^{-1}$ Na, yellow $700\text{--}1500 \mu\text{mol l}^{-1}$ Na, and red $> 1500 \mu\text{mol l}^{-1}$ Na. (d) Regions without likely sodium limitation (brown) due to either a sodium input (aerosol, soil or river) ($> 300 \mu\text{mol l}^{-1}$ Na) or high animal lateral diffusion. Regions with likely sodium limitation (green).

Discussion

Do high coastal sodium concentrations in tropical forests limit plant growth? There are many studies showing reduced productivity in agricultural systems with increased sodium concentrations (Loomis and Conner 1992, Blumwald et al. 2000, Tester and Davenport 2003), but no such studies in tropical forest systems that we are aware of. Therefore, we cannot definitively say that tropical forest production decreases with increased soil sodium concentrations. However, studies have shown that non-halophyte species tend to suffer reduced productivity under high soil sodium concentrations (Loomis and Conner 1992, Blumwald et al. 2000, Tester and Davenport 2003). Therefore, we can constrain our question to: are tropical forests trees broadly non-halophytic? When we average all our leaf nutrient data, we find that sodium is taken up by leaves at high concentrations at a ratio more similar to that of the essential nutrient potassium than the toxic element aluminium. Further, as soil sodium concentrations increase, leaf sodium concentrations increase without any apparent variation at high sodium concentrations (Fig. 1). If tropical trees had an inherent mechanism for selectively reducing Na uptake (characteristic of halophytes), then there would have been a negative relationship between the ratio of leaf to soil K/Na with increased soil Na (Fig. 1). However, this relationship was not present ($p < 0.05$) and we therefore characterize the basin broadly as non-halophytic, which suggests the possibility that sodium concentrations in coastal regions may limit productivity, but this conclusion awaits further experimental evidence. These coastal ecosystems, already some of the most severely altered ecosystems on the planet, may therefore be experiencing additional stress from sodium.

Plants have evolved a variety of ways of reducing the impacts of sodium on productivity, all coming at some cost (Loomis and Conner 1992, Blumwald et al. 2000, Tester and Davenport 2003). For instance, roots 'may be committed to an unnecessarily expensive mechanism of Na extrusion' because of the large electrochemical potential difference – a strategy whose costs increase with the increasing success of keeping Na in the rhizosphere (Tester and Davenport 2003). Complex salt glands, which remove salts through the cuticle of a leaf, have evolved a small number of times in distantly related plants suggesting that mechanisms to exude salts have repeatedly been evolutionarily advantageous in diverse taxa (Hill and Hill 1976). These expensive adaptations indicate that sodium has a very high cost to plant function. However, in all of these strategies, the plant will again encounter the same Na that has been previously exuded, extruded, or stored in vacuoles once the leaf senesces and falls to the base of the tree and thus, the sodium will continue to reduce the fitness of the woody perennial. Given our findings that a) sodium concentrations in coastal regions are very high, and b) that herbivory could potentially be an effective means to remove Na from the territory of a tree, we now pose a hypothesis: could herbivory in fact raise the fitness of plants in sodic and coastal environments, by reducing its long-term Na burden? In other words, might leaf sodium concentrations and leaf defence compounds vary inversely? If a plant reduces its defence compounds, it will more likely be consumed by a herbivore and sodium concentrations will be reduced.

Although logical, there are evolutionary complications with this hypothesis because sodium removal by any individual tree will also benefit the tree's competitors and not burden them with the expense of lost leaf area. Another problem is that herbivory by mega-herbivores can drastically reduce productivity through changes to vegetation structure. For example, along the coasts of Gabon where megafauna remain abundant, woody plants are repeatedly cropped almost to the ground by elephants and other large mammals seeking sodium in the foliage (J. Terborgh pers. comm.).

Sodium concentrations may reach excess levels in certain coastal and sodic ecosystems, but sodium may be a limiting nutrient in other parts of the world (especially the Amazon and Siberia) (Fig. 4). Could this be partially due to the global defaunation, especially of large species, that has extended over the past 10 000 yr? We find total sodium concentrations 10 times higher along the coast than inland in the Amazon basin which is a very large concentration gradient. We had also previously estimated that the lateral diffusion capacity of animals dropped by greater than 98% in the Amazon basin following the Pleistocene extinctions (Doughty et al. 2013). Since the lateral diffusion is a function of both the lateral distribution capacity of the animals and the initial concentration gradient of the nutrient, it is difficult to imagine a scenario where there has not been an impact of the Pleistocene extinctions on global sodium concentration gradients and this is reflected in our simulations (Fig. 2). Therefore, today, animals in inland tropical regions may be more dependent on getting their sodium from salt licks than in the past, possibly because inland leaf vegetation now may have lower sodium concentrations than before.

Our model reduces immensely complex systems to simple herbivores and trees and our results should therefore be viewed with appropriate caution. However, our sensitivity study (Supplementary material Appendix 1, Table A3 and A4) indicates that under all possible variations of the model, the role of large animals is important and the absence of large animal will reduce sodium concentrations in inland regions. One of the largest model uncertainties is how many of the megaherbivores were browsers capable of feeding on trees. Isotopic evidence indicates that in the Amazon region at least two megaherbivores (*Stegomastodon* and *Toxodon*) consumed C3 plants (typically trees) (Franca et al. 2015), but this remains a large uncertainty. Have humans taken over the role of the megafauna as distributors of sodium since we create sodic soils through irrigation and add other nutrients to agricultural systems? Further research is necessary, but we have speculated previously that humans and their domestic animals tend to concentrate versus disperse such nutrients (Doughty 2013, Doughty et al. 2013, 2015), and therefore have not taken over this role.

Therefore, both the Pleistocene extinctions and modern megafauna extirpations may have led to decreased sodium concentrations in inland regions and sodium limitation has been shown in studies to stress animal life (Blair-West et al. 1968). For instance, there is some evidence that sodium supplementation of sheep and cattle increased both weight and lactation which could have increased abundance later (Joyce and Brunswick 1975). Previous studies have found that mammal densities in localities with minimal hunting in the central Brazilian Amazon are much higher in varzea

forests, with higher nutrients (including sodium) than in the terra firme forests (Peres 2000). The discrepancy has been attributed by Peres and others as a consequence of nutrient (N, P, K) deficiencies in interfluvial uplands, but further testing of this assumption remains. In this paper, we suggest that sodium constraints may play a similar role in many inland forests constraining animal abundance. However, this hypothesis remains speculative without further data collection efforts since we know very little about how low sodium concentrations may affect animal abundance.

Overall, we suggest the possibility that there was a delicate interaction between plants and animals controlling ecosystem sodium concentrations that may have become disrupted starting with the Pleistocene extinctions and continuing through today. We have shown such an imbalance in phosphorus following the megafauna extinctions (Doughty et al. 2013, 2015), but here we suggest that the impact on sodium was also important due to the larger intrinsic concentration gradient (a 2–3 fold gradient with phosphorus versus a ~ 10 fold gradient with sodium), although sodium is more soluble than phosphorus leading to a higher loss rate (K). It is unfortunate that just as these important ecosystem processes of large animals are being recognized is when large animals are most rapidly being depleted in the areas where they currently live, with > 60% of central African forest elephants lost in just the last 10 yr (Maisels et al. 2013). Future reserve planning could try to include some coastal access to ensure better distribution of sodium into inland regions. Large animals have long been recognized for their charismatic appeal, but here we show that they also may play an important and previously unrecognized role in maintaining the sodium balance of our planet (Fig. 4).

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References

- Abbas, F. et al. 2012. Roe deer may markedly alter forest nitrogen and phosphorus budgets across Europe. – *Oikos* 121: 1271–1278.
- Baraloto, C. et al. 2011. Disentangling stand and environmental correlates of aboveground biomass in Amazonian forests. – *Global Change Biol.* 17: 2677–2688.
- Baraloto, C. et al. 2012. Using functional traits and phylogenetic trees to examine the assembly of tropical tree communities. – *J. Ecol.* 100: 690–701.
- Barnosky, A. D. et al. 2004. Assessing the causes of Late Pleistocene extinctions on the continents. – *Science* 306: 70–75.
- Blair-West, J. R. et al. 1968. Physiological morphological and behavioural adaptation to a sodium deficient environment by wild native Australian and introduced species of animals. – *Nature* 217: 922.
- Blumwald, E. et al. 2000. Sodium transport in plant cells. – *Bba-Biomembranes* 1465: 140–151.
- Botkin, D. B. et al. 1973. Sodium dynamics in a northern ecosystem. – *Proc. Natl Acad. Sci. USA* 70: 2745–2748.
- Carbone, C. et al. 2005. How far do animals go? Determinants of day range in mammals. – *Am. Nat.* 165: 290–297.
- Croll, D. A. et al. 2005. Introduced predators transform subarctic islands from grassland to tundra. – *Science* 307: 1959–1961.
- Damuth, J. 1987. Interspecific allometry of population-density in mammals and other animals – the independence of body-mass and population energy-use. – *Biol. J. Linn. Soc.* 31: 193–246.
- de Magalhães, J. P. and Costa, J. 2009. A database of vertebrate longevity records and their relation to other life-history traits. – *J. Evol. Biol.* 22: 1770–1774.
- Dirzo, R. et al. 2014. Defaunation in the Anthropocene. – *Science* 345: 401–406.
- Doughty, C. E. 2013. Preindustrial human impacts on global and regional environment. – *Annu. Rev. Environ. Resour.* 38: 503–527.
- Doughty, C. E. et al. 2013. The legacy of the Pleistocene megafauna extinctions on nutrient availability in Amazonia. – *Nat. Geosci.* 6: 761–764.
- Doughty, C. E. et al. 2015. Global nutrient transport in a world of giants. – *Proc. Natl Acad. Sci. USA* doi: 10.1073/pnas.1502549112
- FAO 2013. Digital soil map of the World. – <www.fao.org/geonetwork/srv/en/metadata.show?id=14116>.
- Fisher, J. B. et al. 2009. The land-atmosphere water flux in the tropics. – *Global Change Biol.* 15: 2694–2714.
- Fortunel, C. et al. 2014. Environmental factors predict community functional composition in Amazonian forests. – *J. Ecol.* 102: 145–155.
- Franca, L. D. et al. 2015. Review of feeding ecology data of Late Pleistocene mammalian herbivores from South America and discussions on niche differentiation. – *Earth-Sci. Rev.* 140: 158–165.
- Furch, K. and Klinge, H. 1989. Chemical relationships between vegetation, soil and water in contrasting inundation areas of Amazonia. – Special publications of the Brazilian Ecological Society.
- Gaillardet, J. et al. 1999. Global silicate weathering and CO₂ consumption rates deduced from the chemistry of large rivers. – *Chem. Geol.* 159: 3–30.
- Golley, F. B. et al. 1978. Elemental concentrations in tropical forests and soils of northwestern Colombia. – *Biotropica* 10: 144–151.
- Grattan, S. R. and Grieve, C. M. 1992. Mineral element acquisition and growth-response of plants grown in saline environments. – *Agric. Ecosyst. Environ.* 38: 275–300.
- Hill, A. and Hill, B. 1976. Mineral ions. – In: Lüttge, U. and Pitman, M. G. (eds), *Encyclopedia of plant physiology*, vol. 2. Transport in plants. II. Part B. Tissues and organs. Springer, pp. 225–243.
- Joyce, J. P. and Brunswick, L. C. F. 1975. Sodium supplementation of sheep and cattle fed lucerne. – *N. Z. J. Exp. Agric.* 3: 299–304.
- Kaspari, M. et al. 2008. On the biogeography of salt limitation: a study of ant communities. – *Proc. Natl Acad. Sci. USA* 105: 17848–17851.
- Kaspari, M. et al. 2009. Sodium shortage as a constraint on the carbon cycle in an inland tropical rainforest. – *Proc. Natl Acad. Sci. USA* 106: 19405–19409.
- Kurlansky, M. 2003. *Salt: a world history*. – Vintage Press.
- Lavery, T. J. et al. 2010. Iron defecation by sperm whales stimulates carbon export in the Southern Ocean. – *Proc. R. Soc. B* 277: 3527–3531.
- Lindsey, E. and Barnosky, A. 2008. Timing of extinctions among Late-Pleistocene megamammal taxa in South America. – *J. Vertebr. Paleontol.* 28: 106A.
- Loomis, R. S. and Conner, D. J. 1992. *Crop ecology: productivity and management in agricultural systems*. – Cambridge Univ. Press.

- Maisels, F. et al. 2013. Devastating decline of forest elephants in central Africa. – PLoS One 8: e59469.
- Maron, J. L. et al. 2006. An introduced predator alters Aleutian Island plant communities by thwarting nutrient subsidies. – Ecol. Monogr. 76: 3–24.
- Marschner, H. 1995. Mineral nutrition of higher plants. – Academic Press.
- McDonald, R. L. et al. 1982. Estimation of atmospheric sea salt dry deposition – wind-speed and particle-size dependence. – J. Geophys. Res. 87: 1246–1250.
- Okubo, A. and Levin, S. A. 2001. Diffusion and ecological problems: modern perspectives. – Springer.
- Ovaskainen, O. and Crone, E. E. 2009. Modeling animal movement with diffusion. – In: Cantrell, S. et al. (eds), Spatial ecology. Chapman and Hall/CRC, pp. 63–83.
- Patino, S. et al. 2012. Coordination of physiological and structural traits in Amazon forest trees. – Biogeosciences 9: 775–801.
- Peres, C. A. 2000. Effects of subsistence hunting on vertebrate community structure in Amazonian forests. – Conserv. Biol. 14: 240–253.
- Quesada, C. A. et al. 2010. Variations in chemical and physical properties of Amazon forest soils in relation to their genesis. – Biogeosciences 7: 1515–1541.
- Rees, P. S. 1983. Synchronization of defecation in the African elephant (*Loxodonta africana*). – J. Zool. 201: 581–585.
- Roman, J. and McCarthy, J. J. 2010. The whale pump: marine mammals enhance primary productivity in a coastal basin. – PLoS One 5: e13255.
- Scott, J. P. 1969. Introduction to animal behaviour. – In: Hafez, E. S. E. (ed.), The behaviour of domestic animals. Bailliere, Tindall and Cassel, pp. 3–21.
- Skellam, J. G. 1951. Random dispersal in theoretical populations. – Biometrika 38: 196–218.
- Sofiev, M. et al. 2011. A regional-to-global model of emission and transport of sea salt particles in the atmosphere. – J. Geophys. Res. 116: D21302.
- Stallard, R. F. 2012a. Atmospheric inputs to watersheds of the Luquillo Mountains in eastern Puerto Rico. – In: Murphy, S. F. and Stallard, R. F. (eds), Water quality and landscape processes of four watersheds in eastern Puerto Rico. U. S. Geological Survey Professional Paper 1789-D, pp. 85–112.
- Stallard, R. F. 2012b. Weathering, landscape equilibrium, and carbon in four watersheds in eastern Puerto Rico. – In: Murphy, S. F. and Stallard, R. F. (eds), Water quality and landscape processes of four watersheds in eastern Puerto Rico. U. S. Geological Survey Professional Paper 1789-H, pp. 199–248.
- Stallard, R. F. and Edmond, J. M. 1981. Geochemistry of the Amazon. 1. Precipitation chemistry and the marine contribution to the dissolved-load at the time of peak discharge. – J. Geophys. Res. 86: 9844–9858.
- Stevenson, P. R. and Guzman-Caro, D. C. 2010. Nutrient transport within and between habitats through seed dispersal processes by woolly monkeys in north-western Amazonia. – Am. J. Primatol. 72: 992–1003.
- Terborgh, J. and Estes, J. A. (eds) 2010. Trophic cascades: predators, prey, and the changing dynamics of nature. – Island Press.
- Tester, M. and Davenport, R. 2003. Na⁺ tolerance and Na⁺ transport in higher plants. – Ann. Bot. 91: 503–527.
- Weeks, H. P. and Kirkpatrick, C. M. 1976. Adaptations of white-tailed deer to naturally occurring sodium deficiencies. – J. Wildl. Manage. 40: 610–625.
- Weeks, H. P. and Kirkpatrick, C. M. 1978. Salt preferences and sodium drive phenology in fox squirrels and woodchucks. – J. Mammal. 59: 531–542.
- Weir, J. S. 1972. Spatial-distribution of elephants in an African National Park in relation to environmental sodium. – Oikos 23: 1–13.
- West, G. B. et al. 1997. A general model for the origin of allometric scaling laws in biology. – Science 276: 122–126.
- Wolf, A. et al. 2013. Lateral diffusion of nutrients by mammalian herbivores in terrestrial ecosystems. – PLoS One 8: e71352.
- Young, H. S. et al. 2010. Plants cause ecosystem nutrient depletion via the interruption of bird-derived spatial subsidies. – Proc. Natl Acad. Sci. USA 107: 2072–2077.

Supplementary material (Appendix ECOG-01589 at <www.ecography.org/appendix/ecog-01589>. Appendix 1.