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Biotic Translocation of Phosphorus: The Role of Deer in Protected Areas

Werner T. Flueck^{1,2,3}

¹ CONICET (National Council for Scientific Research), C.C. 176, 8400 Bariloche, Argentina; E-Mail: wtf@deerlab.org; Tel./Fax: +54-2944-467345

² Instituto de Análisis de Recursos Naturales, Universidad Atlántida, 7600 Mar del Plata, Argentina

³ Swiss Tropical Institute, University Basel, 4002 Basel, Switzerland

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Abstract: Biogeochemical cycles are cornerstones of biological evolution. Mature terrestrial ecosystems efficiently trap nutrients and certain ones are largely recycled internally. Preserving natural fluxes of nutrients is an important mission of protected areas, but artificially leaky systems remain common. Native red deer (*Cervus elaphus*) in the Swiss National Park (SNP) are known to reduce phosphorus (P) in preferred feeding sites by removing more P than is returned with feces. At larger scales it becomes apparent that losses are occurring due to seasonal deer movements out of the SNP where most deer end up perishing. Thus, the SNP contributes to producing deer which translocate P to sink areas outside the SNP due to several artificial factors. An adult female dying outside of SNP exports about 1.8 kg of P, whereas a male dying outside of SNP at 8 years of age exports 7.2 kg of P due also to annual shedding of antlers. Averaged over the vegetated part of the SNP, the about 2,000 deer export 0.32 kg/ha/yr of P. Other ungulate species using the SNP and dying principally outside of its borders would result in additional exports of P. Leakiness in this case is induced by: a) absence of the predator community and thus a lack of summer mortalities and absence of several relevant non-lethal predator effects, b) hunting-accelerated population turnover rate, and c) deaths outside of SNP principally from hunting. The estimated export rate for P compares to rates measured in extensive production systems which receive 10-50 kg/ha/yr of P as fertilizer to compensate the losses from biomass exports. Assumptions were made regarding red deer body weight or population turnover rate, yet substituting my estimates with actual values from the SNP would only affect somewhat the magnitude of the effect, but not its direction. The rate of P loss is a proxy for losses of other elements, the most critical ones being those not essential

to autotrophs, but essential to heterotrophs. High deer turnover rates combined with accelerated biomass export warrants detailed mass balances of macro and micro nutrients, and studies of biogeochemical cycles in protected areas are essential if preserving natural processes is a mandate.

Keywords: Cervus elaphus; Phosphorus; Biogeochemical cycle; Protected areas; Biomass export.

1. Introduction

The dynamic of biogeochemical cycles is a cornerstone of biological evolution [1]. As pristine ecosystems tend to be nearly closed with regard to several nutrients, many protected areas such as national parks have the explicit obligation to preserve as much as possible the ecological stoichiometry, that is natural patterns of energy and material flows. This is based on the tenet that the recent biodiversity is a result of patterns of energy and material flows established during the development of the ecosystem together with the prevailing patterns of natural disturbances. Sustainability in this case can be defined as including those anthropogenic activities which do not result in a deviation of system development as occurs under pristine conditions. Clearly, for most areas such conditions no longer occur and there have been numerous anthropogenically induced forces at work, like air pollution, extermination of native species or introduction of alien species. Many current efforts are thus directed to revert such recognized impacts and aim at returning closer to pristine conditions. However, other ecological megatrends like removal and export of biomass in relation to biogeochemical cycles, have received less attention.

As ecosystems mature, many nutrients become mainly recycled internally, and the pool of such nutrients stored in biomass becomes larger while the nutrient pool in soil becomes increasingly reduced compared to the biomass [2-4,57]. In fact, release of such nutrients from weathering of rock is insignificant in relation to what the maximal standing biomass needs and thus, mature forest systems for instance may take thousands of years to develop through efficient biogeochemical cycling with increasing nutrient accumulation [2,3,5,6].

The biogeochemical cycle of phosphorus (P) in terrestrial systems occupies a key position currently and in the near future due to the global scale of human-induced alterations in its dynamics, which basically having made the cycle become predominantly an open one [7-8]. The importance on the one hand surges from our reliance on production systems to channel organic material into far removed centers of human consumption, mainly as food, fiber, wood products and fuel. Production systems based on forestry, animal husbandry and agriculture all rely on local soil P reserves, but in all systems the continued import of P has been necessary, most notoriously in agriculture [9-12]. The current emphasis to increase production of biofuels through agriculture and forestry in response to the energy crisis represent an additional enormous demand for P fertilizer, resulting in competition with food production system. On the other hand, areas exploited through extensive production (range land, silvicultural and silvopastoral systems) are also important as they often support wildlife. Thus, the

depletion of soil P reserves not only affects the economy of extensive production systems, but also affects wildlife and thereby ecosystem processes.

Central to the biogeochemical cycle of P is its virtual immobility which, in absence of harvesting, results in nearly closed local cycles and often makes it a limiting factor [8,15,45]. The concentration factor for soil-plant systems is possibly the highest known [46]: terrestrial plants and zoomass contain 500-550 and 30-50 million tons of P, respectively, in contrast to only 50 million tons of inorganic and organic P in soils [8]. As natural input and output rates are minimal, developing systems slowly accumulate P until a steady state is reached and biological recycling is maximal both at the organismal and ecosystem levels [3,4,6,39]. This secondary cycling of organic P has rapid turnover times of just a few days to a few years and cycling must be highly efficient: terrestrial plants take up 40-100% more P than exists in soil as organic and inorganic P [8]. Importantly, productive systems involving harvest and export of crops, trees and animals have all been recognized to remove more P than would be removed under natural conditions, and in excess of the limited inputs, depleting reserves in the process and thus making the system unsustainable. For that reason P has been termed life's bottleneck by Asimov [46], a fact published in Nature earlier in 1942 [47, see also 6,48].

In this paper I examine attributes of the P cycle as they relate to sustainability in protected areas. As many protected areas are islands within a matrix of production systems, the mandate to preserve natural patterns of energy and mineral flows may not be possible to achieve. For several reasons, protected areas are frequently equivalent to extensive production systems, and as such would require the same type of active management of biogeochemical cycles as applied in production systems, namely through fertilizer application.

2. Materials and Methods

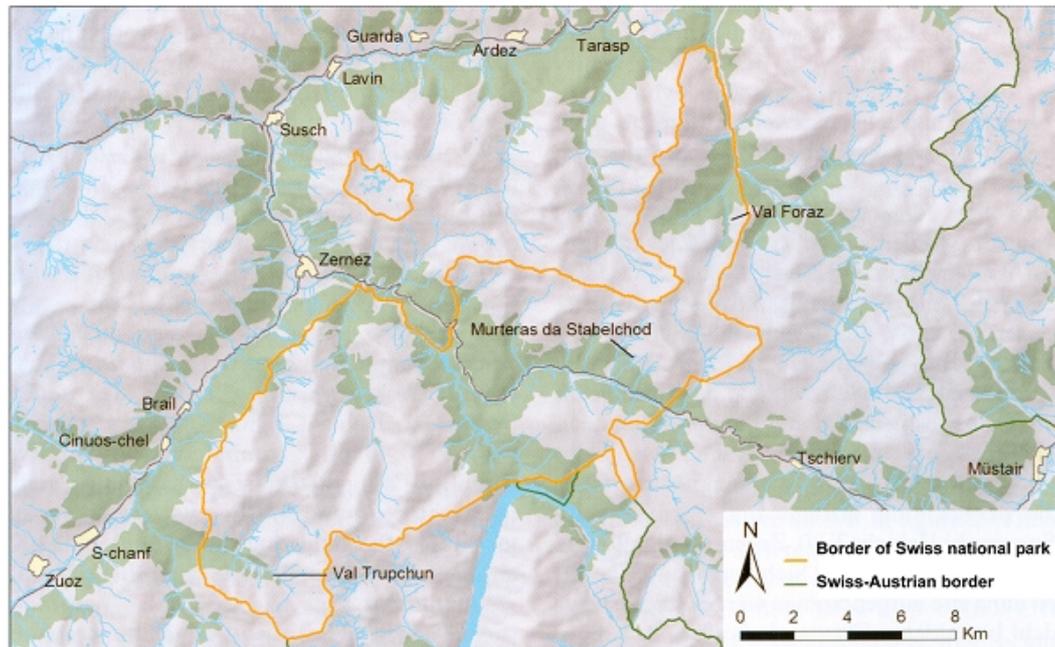
I review information regarding a case study from the Swiss National Park (SNP), based on a system with native red deer (*Cervus elaphus*) as the major herbivore, which compared P removal in aboveground biomass due to foraging with P input due to deposition of feces [13]. I review data on deer body composition regarding P, population density in the park, and movement and mortality patterns to construct a mass balance for P at the scale of the deer population. The weight of male red deer heads included the cranium, and according to the international CIC formula, up to 700 g are deducted for the 'long-nose cut' [14]. To estimate the weight of antlers I assume that the remaining skull weighs 300 g and thus I deducted 1 kg from registered head weights.

2.1. Description of the Swiss National Park

The 172 km² sized SNP is situated between about 1,400 and 3,173 m a.s.l (Figure 1, from [16]). The SNP was founded in 1914 and due to being a rigorously protected area (category Ia IUCN), there were no further agricultural, forestry or hunting activities in order to permit strict protection of ecosystem processes. Visitors have to use a restricted network of trails which are closed in winter. The SNP is 48% covered with vegetation, including 28% as forest or forest-like communities, and 20% as

subalpine and alpine grassland. The remaining portion consists of rocks, gravel fields, and water bodies.

Figure 1. Location, topography and forested areas (green) of the Swiss National Park.



3. Results

3.1. Red Deer as an Agent of P Translocation in the Swiss National Park

Schütz *et al.* [13] studied native red deer as the major herbivore in a national park study site, a grazing lawn of 10.7 hectares. They looked at concentrations of P in plants and soils from preferred short-grass and non-preferred tall-grass vegetation, and compared P removal of aboveground biomass due to grazing with P input due to deposition of feces. The proportion of heavily grazed short-grass community increased with increasing soil-P pool and thus, P removal through grazing increased as well. As P return rates from defecation also increased with increasing soil-P pool, it resulted in a constant mean net P loss of 0.083 kg/ha/yr independent of both soil-P pool and vegetation type. It was concluded that the net rate of P loss was likely too small to explain the observed changes in vegetation composition and that the grazing patterns of red deer directly induced these successions, but they also considered the possibility that long-term, small net soil-P losses indirectly drive plant succession from short-grass to tall-grass vegetation, because nutrient depletion could reduce grazing pressure in short-grass vegetation and enable the characteristic tall-grass species to establish.

3.2. Phosphorous Translocations at the Scale of the Red Deer Population

In their analysis, Schütz *et al.* [13] made the implicit assumption that the red deer using the study site are always the same individuals, as they made no reference to the biological cycle of red deer in

this region. Woodmansee and Duncan [15] showed that the P cycle in grassland systems is nearly closed based on mass balance without harvests, and Schütz *et al.* [13] explicitly adopted the assumption that there are no other existing P sinks or P sources. They found no transfer of P between the short-grass and tall-grass portions in the 10.7 ha study site. Possibly some non-returned P was deposited in the surrounding forests or alpine grasslands as summer home ranges of red deer in the park vary between 350-500 ha [16], but then deer would certainly forage in those areas as well and deposit resulting feces while feeding back on the study site. More likely, non-returned P was exported from the SNP via animal displacements and differential mortality.

In general, female red deer, having survived winter conditions, would follow the plant phenology to reach their summer range. There they will spend their most productive part of the annual cycle, finding superabundant food which allows not only to also feed the new calf, but regain fat reserves for the following winter season. From a nutritional perspective, there are few if any reasons to anticipate mortalities on the summer range. Furthermore, natural risk factors have gone extinct in the park, as none of the large predators is present, thus eliminating this mortality factor. Schütz *et al.* [13] did not mention the use of their study site by other herbivores, thus I assume that it was only used by red deer. Furthermore, there is no competing domestic livestock in the park and the only factors possibly resulting in summer mortalities are accidents or rare diseases and, due to the lack of large predators, overabundance of the native herbivore community (see [17]). Mortalities in this population are thus foremost during winter in ranges outside of SNP [59] where also hunting is applied for population management (Figure 2). In the following I thus construct a mass balance for P at the scale of the red deer population.

Figure 2. Red deer driven in winter to low elevations and towns outside the Swiss National Park.



3.3. Density of Red Deer in the Swiss National Park

Since the reappearance of red deer in the SNP area in about 1917, the population increased to maximal densities in the 1980s, when densities in the vegetated parts of the park averaged 36.4 deer/km² [18]. Some episodes of winter dieoffs due to overabundance and subsequent more intense hunting programs kept the density at lower levels thereafter. Approximately 2,000 red deer now remain in the park, mainly during the summer where they utilize about 8,500 ha of vegetated park area, amounting to about 23.5 deer/km² [13,18].

3.4. Phosphorus in Female Red Deer

For the purpose of the present paper, I evaluate potential reasons for the negative P balance observed in the park study site, and also look at a scale beyond the special grazing lawn which was a minor portion of the area used by the deer population. In mule deer (*Odocoileus hemionus*), 10% of body weight was bone tissue [19], similar to red deer [20]. Bones of white-tailed deer (*Odocoileus virginianus*) had 28.6% moisture and contained 58.5% ash (dry basis) of which 30.5% was P [21]. The soft tissues contain another 15% of P in addition to bone P [8]. Based on adult female red deer in the Argentine national park Nahuel Huapi (NPNH, Flueck unpublished), I use 120 kg as average live weight (n = 7). The bones and soft tissue would thus contain 1.76 kg of P, representing 1.47% of body weight.

3.5. Mass Balance for P for Female Red Deer

First, as elaborated above, female red deer do not tend to die on the summer range which was studied, but they die elsewhere. There are no predators, there is no hunting, it is the most productive period of the year, thus mortality cases on the summer range would be rare. According to Schütz *et al.* [13] the population size remained constant during their 5-year study period. This is explained by deer leaving the SNP, where they are exposed to the regional hunting program which, among other things, aims to keep the population at a steady low level to avoid repeats of dieoffs and overabundance in general [16,18]. I posit that most all deer using the studied feeding area die at considerable distance from the site.

Second, preferred feeding areas would attract numerous deer. In areas with high red deer numbers in Patagonia (5 × 5 km) we estimated an average of about 100 red deer/km² which translated into big mobs concentrating at preferred short-grass sites [55]. I assume that the area studied by Schütz *et al.* [13] was used by 15 adults and subadults, mainly female red deer. I assume that the population is managed to be in good body condition, and thus has an annual population growth rate of 30% (reaching 35% in New Zealand, [23]). Therefore, I expect that at least 4.5 adult deer would die on winter ranges each year for a steady-state population. As a consequence, each year this particular site would lose some 3.96 kg of P from 2.25 females dying in remote sites and at least 3.96 kg of P from 2.25 young males dispersing to other sites (assuming even birth sex ratio). Whereas the average net P loss was calculated as 0.083 kg P/ha/yr based on removal of forage and returns from feces, the actual

loss from deer turnover constitutes a loss of 0.74 kg P/ha/yr from the system, or nine times more than the estimate based on this forage patch [13].

If on the other hand the study site lost 0.89 kg of P/yr ($10.7 \text{ ha} \times 0.083 \text{ kg P/ha/yr}$, [13]), it would account for the annual loss of only 61 kg of deer biomass, assuming no losses due to other factors like soil acidification, erosion etc. At a population growth rate of 30% this would indicate a deer biomass using this site of about one female producing a calf which dies or disperses each year. This feeding patch is obviously utilized by many more deer. In fact, the reported biomass consumed by deer, assuming 40% of the site to be short grass (Figure 1b in [13]), amounts to 18.8 kg/day dry matter consumed, which corresponds to about 1,363 kg of deer biomass [24]. The reported loss of 0.083 kg P/ha/yr [13], therefore, does not coincide with the reported grazing pressure nor my estimated population turnover rate. The discrepancy between the measured loss of 0.89 kg of P and the loss of 7.92 kg of P estimated based on population turnover likely is the result from deer regularly feeding also in other proportions of their home range where they extracted P, and uneven distribution of feces.

3.6. Mass Balance for P for Male Red Deer

It is common that adult male red deer do not summer in the same areas as female groups, and the same holds true for the SNP [18]. Although some males may remain in the park, particularly during mild winters, most leave the park where they are subjected to hunting programs. Not only are mature males about two times heavier than females [56], but in addition they annually produce antlers. Based on adult male red deer hunted in NPNH between 2001 and 2008, average antler weight is 6.0 kg (SE = 0.1 kg, n = 151, Flueck unpublished). Average P content in fresh antlers based on reported moisture content and P in ash is 13.5% [21,25,26]. Therefore, a hunted average male in the NHNP would have about 0.81 kg of P in his antlers. An adult male hunted far from his summer range thus might represent 3.52 kg of P in his body plus 0.81 kg in antlers, or 4.33 kg of P exported from the summer range. I am not familiar with the situation of shed antlers in areas around the SNP, but in the NPNH there are large quantities of antlers being collected, mostly outside of the park but some also inside, and used for commercial purposes. Using the average age of 8 years (Se = 0.3, n = 136) for males hunted in the NHNP, a male would shed about 21 kg of antlers before dying with his last set of antlers at 8 years old, representing about 2.84 kg of P in shed antlers. Thus, the male portion of the red population in the SNP also contributes significantly in translocating P through their most common path of death which tends to be outside of the park (hunting and winter deaths) and through shedding antlers, also often outside of parks. A male shedding antlers and dying outside of SNP would on average have exported 407% more P than a female. As a rough estimate from graphs in Haller [18] there has been an increasing number of red deer being shot outside of the SNP, numbering hundreds of deer. The estimated 2,000 red deer summering in the SNP (www.nationalpark.ch) would result in some 600 deer dying annually (based on 30% annual population growth rate), mainly far away from where they were feeding.

3.7. Red Deer Uptake of P on Winter Ranges and Its Contribution to the Summer Range Balance

The topography and location of the SNP make it a highly seasonal environment which determines the annual cycle of plants and red deer (Figure 1). Major adaptations by red deer include the drastically reduced voluntary food intake in winter as an obligatory response to the photoperiod, which can be induced several times per year under manipulated photoperiod cycles [27,28]. As a consequence, body growth ceases during the winter and deer lose body weight due to catabolizing fat and protein reserves [28,29]. As body growth is absent during winter, there is no accumulation of P in body tissues. Gravid females also would incorporate little new P as the main growth spurt of the fetus is during the last trimester of gestation [30]. On the other hand, loss of body weight during winter due to catabolism can amount to 30% of autumn body weight, and thus represents a net flux of P assimilated on summer range and lost during the winter season [26]. Because fat is the main tissue lost during winter, most P is contained in bones, and forage available during winter is low in P, I assume that the winter loss of P is small in magnitude and do not consider it for the following mass balance calculations.

3.8. Mass Balance for Total P Export from of the Swiss National Park due to Red Deer

Most of the 2,000 red deer leave the SNP to remain in lower winter ranges [18,59], and thus most of them die outside of the SNP. Antlers would be shed outside the SNP as most males also leave the SNP in winter. Assuming management aiming at even sex ratios and good physical condition, a large proportion of death would occur among adults of both sexes. The total annual export of P from these approximately 600 deer dying outside the SNP thus amounts to 2,679 kg of P (Table 1). Catabolism of the remaining live deer on the winter range would result in additional P translocated from summer to winter range, by excreting more P than taken up through forage.

The mass balance for P in a heavily used summer feeding area was an annual loss of 0.083 kg P/ha based on forage removed and feces deposited [13]. Possible sinks include runoff or deer defecating in other portions of their summer home range and thus merely shifting some P locally. However, lactating and growing animals also would accumulate P in their bodies with the final destiny of P determined by the site of death, and my calculations thus address the inescapable export of P from the SNP which is substantially larger by 380%, and averages to 0.32 kg/ha/yr of P across the vegetated portion of the SNP. As some of the vegetated portion of the SNP might not be used by red deer, local export rates would be expected to be higher. There are other species like roe deer (*Capreolus capreolus*) and chamois (*Rupicapra rupicapra*) which are hunted outside of the SNP, yet might spend considerable time foraging in the SNP. In that case these herbivores would contribute to an even higher rate of P export from the SNP. As the study site used by Schütz *et al.* [13] had an artificially enriched P soil reserve, the majority of the SNP would have substantially less soil reserves [31], and the calculated rate of export of P (based only on red deer) would be expected to be of more relative importance in the remaining portion of the park.

Table 1. Parameters used for analyzing phosphorus translocation in the Swiss National Park (SNP).

Variable	Parameter	Source
<i>Deer population in the SNP as summer range</i>		
total number of deer	2000	[13,18]
vegetated area	8,500 ha	[18]
population growth rate	30%, estimate, as it can be 35%	[23]
winter range	Mainly outside SNP	[18]
<i>Red deer, national park Nahuel Huapi, Argentina</i>		
female body weight	120 kg (n = 7)	Flueck unpubl.
male body weight	240 kg	
<i>Phosphorus in female red deer</i>		
bone mass	10% of body weight	[19,20]
[P] in wet bone	12.74%	[21]
[P] in soft tissue	15% above bone content	[8]
[P] in whole body	1.47%	[8,19,20,21]
P in female of 120kg	1.76 kg	[8,19,20,21]
<i>Phosphorus in male red deer</i>		
[P] in wet bone	12.74%	[21]
[P] in soft tissue	15% above bone content	[8]
[P] in fresh antler	13.5%	[21,25,26]
antler weight, 8 year old male	6.0 kg (n = 151)	Flueck unpubl.
lifetime shed antlers to 7 years of age	21 kg	Flueck unpubl.

3.9. How Does the Export Rate of 0.32 kg/ha/yr of P Estimated for the SNP Compare to Other Systems?

A comparison of fluxes reported from extensive production systems based on livestock and forestry provides a reference point with regards to my estimates for the SNP system (Table 2). Extensive sheep production in Scotland removed 0.23 kg P/ha/yr, assuming 1% P in live weight, and such grasslands received 16 kg of P/yr as fertilizer to compensate losses [32]. Extensive cattle production on range lands in San Luis, Argentina removed 0.3 kg/ha/yr of P which was considered unsustainable if not accompanied with fertilizer [33,34]. Furthermore, even the most fertile range land soils known, like those of La Pampa in Argentina, show an increased frequency of soils deficient in P due to absent or insufficient fertilizer application, and overall export of P from livestock products was 12% larger than inputs from fertilizer [35]. Also, only 20 years of extensive cattle grazing in the province of Buenos

Aires, without applying fertilizer, resulted in a measurable reduction in extractable P, and in 50 years it fell by 67% from 45 ppm to 15 ppm [35]. The amount of P removed in sheep or cattle products accounted for 15-20% of the P taken up by the animals which was compensated for by application of 10-50kg P/ha/yr fertilizer to range land [35,36]. Bishopp proposed in 1946 [37] the need for careful monitoring of pastoral lands in Ireland as they experienced a annual loss of 25,000 tons of tricalcium phosphate due to range cattle exports, because imports of phosphate fertilizer had been reduced through the war by 75%.

Based on forests studied throughout the US, harvest of only logs removed 0.08 to 1.02 kg/ha/yr whereas whole-tree harvest removed 0.24 to 1.75 kg/ha/yr of P. These harvested systems lost P regardless of harvest intensity and were considered unsustainable [38]. Whole-tree harvest in other forests removed 20-50kg/ha or half, if only logs were removed [39], and Heilman and Norby [40] reported on forest harvesting which required a fertilizer input of 15-30 kg/ha/yr of P to compensate exports.

Table 2. Comparison of phosphorus fluxes among various extensive production systems.

Fluxes of phosphorus in the SNP and in other extensive production systems				
Harvest scheme	Loss of P from biomass export		Input as P fertilizer	Source
	kg/ha/yr	total kg/ha	kg/ha/yr	
SNP, red deer movement	0.32			this study
sheep, Scotland	0.23		16	[32]
cattle, Alps, currently	0.22			[58]
cattle, Alps, traditionally	0.30			[58]
cattle, Argentina	0.30			[33,34]
sheep, cattle	15-20% of P uptake		10-50	[35,36]
cattle, no fertilizer	extractable P fell 67% in 50 years, from 45 to 15 ppm			[35]
tree log harvest	0.08 - 1.02			[38]
		10 – 25 per harvest	15 - 30	[39,40]
whole-tree harvest	0.24 - 1.75			[38]
		20 – 50 per harvest	15 - 30	[39,40]

4. Discussion

Based on the net loss of P by native red deer grazing in the SNP, Schütz *et al.* [13] concluded that P reserves in the study site would likely become depleted only in periods of several thousand years. However, while true for the small study area with artificially high soil P reserves, it does not hold for the SNP area because the scale of processes reaches beyond the boundary of this protected area. I show that the P cycle is significantly open, and the SNP is effectively a production system. Other protected areas like the NPNH have even more leaky nutrient cycles, because apart from a similar

situation with red deer, they also have substantial livestock grazing and biomass export (Flueck unpublished).

Local translocation of P may influence successional stages in the immediate plant community and affect other biota [41,58]. However, far-ranging herbivores combined with geographically biased mortality patterns can result in important directional fluxes of nutrients which end up in artificial sink areas. There is no doubt that if the large predator community would still be intact in the SNP, habitat use by red deer and thus translocations of nutrients would be different. Besides the many ecologically important non-mortal effects exerted by predators on their prey, like modifying feeding behavior [22,42,43], each kill on the summer range would dissipate the nutrients contained in the prey in that same environment and contribute to local cycling, an important ecosystem process currently absent in the SNP. For instance, significantly increased P concentrations in soils were detectable for several years at sites of ungulate carcasses, creating different vegetation patches which were then more intensely used by ungulates and likely created a feedback loop by resulting in higher mineral input from urine and dung [60]. Similarly, the effect on nutrient cycles from the harvest of wild kangaroo (*Macropus rufus*) was substantially reduced by leaving offcuts (e.g. head, stomach, entrails, legs, tail, offspring) at the kill site, and this contribution of the kangaroo industry to soil nutrient retention and cycling was contrasted with the nutrient mining through the export of domestic livestock from the Australian rangelands [61].

Red deer incorporating and accumulating nutrients during growth on summer ranges, but dying in some distant winter range or shedding antlers in distant places, effectively remove elements from the summer range. This process can be artificially accelerated by eliminating mortality factors on the summer range (predation), by hunting outside of the park area which increases the deer population turnover rate and also creates an artificial sink, or by allowing densities to reach levels where herd condition is low enough to cause excess winter mortalities outside of the park (through lack of predation and inadequate substitution by hunting). High deer density certainly accelerates the mineral turnover rate [44], and thus mineral export rates if animals are removed from the system.

4.1. The Importance of the Macronutrient Phosphorus

First, P is a rather immobile element and often a limiting factor as evidenced by terrestrial plants taking up much more P than exists in soils as organic and inorganic P [8,15,45]. Under minimal natural input and output rates, ecosystems often accumulate P until a steady state is reached and biological recycling is maximal both at the organismal and ecosystem levels [3,4,6,39].

Second, productive systems involving harvest and export of crops, trees and animals are known to deplete reserves of P and make the system unsustainable [46-48, also see 6].

Third, herbivores in production systems remove P in excess of natural inputs [47,49-51,58]. In fact, P is usually the first nutrient which constrains the livestock carrying capacity of land and a recent review about livestock production in Asia revealed that 37.3% of the area has a severe P deficit (> 4.4 kg/ha/yr) and another 39.1 % of the area falls between having a moderate deficit or moderate surplus [52]. Thus, P is probably the nutrient most frequently given as a supplement to rangeland ruminants [53].

Finally, export rates of P as estimated for the red deer using the SNP compare to extensive livestock and forest production systems which, however, are often receiving P fertilizer for compensating the export of P. Extensive production systems not receiving P fertilizer have been shown to become depleted over time [35,58]. Although I made several assumptions such as regarding red deer body weight or population turnover rate, I posit that the current land use practiced in the SNP is not sustainable in terms of P, and substituting my estimates with actual values would only affect somewhat the magnitude of the effect, but not its direction. Intensive as well as extensive production systems are recognized to be depending on P fertilizer input. Current trends to intensify the production of food, energy crops and forest products for energy are increasingly dissipating P and causing increased demands on declining non-renewable P reserves [7]. Non-profit protected areas subjected to export of wild or domestic livestock thus are required to replace certain lost minerals through fertilizer application. Given the constraints from low operating budgets of many protected areas, increasing costs of P, and costly application of fertilizer at the landscape level, protected area management should aim at reducing the net loss of minerals by promoting local cycling patterns. If animals (domestic, native or exotic wild species) are to be harvested, only a minimal part of the animal should be removed, such as trophies or meat cuts [60,61]. Reconstituting a complete and thus effective predator community might work, but in cases of small size as with the SNP, it might not be feasible. In this case hunting in the national park as a replacement for the lack of the predator community might be an acceptable alternative and more natural than the application of mineral fertilizer. Undoubtedly, any beneficiary of products produced in protected ecosystems should be made responsible for covering the resulting externalities: the cost to replace nutrients exported in excess of the capacity of natural replacement.

4.2. General Implications

Although the response of vegetation often serves as a proxy to assess bioavailability of certain nutrients, this approach fails for elements only needed by animals, particularly mammals, or needed at higher concentrations by animals [54]. On the other hand, elements like P can serve as a proxy to estimate fluxes of other as of yet unstudied elements.

In conclusion, high turnover rates of herbivore biomass combined with artificially accelerated biomass export rates warrants detailed studies of mass balances of macro and micro nutrients. The study of biogeochemical cycles in protected areas is essential if preserving natural processes is a mandate. It is a rather neglected issue for many protected areas including National park, for instance in South America, where park areas are exploited through maximal raising of livestock or hunting of invasive ungulates, all of which entail an important leak of nutrients from the protected areas.

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