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Response to Newton *et al*. 2009. “Toward Integrated Analysis of Human Impacts on Forest Biodiversity: Lessons from Latin America”

Evolution of Forest Systems: the Role of Biogeochemical Cycles in Determining Sustainable Forestry Practices

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ABSTRACT. The exploitation of natural resources such as forests leads to sustainable forest management (SFM). The key question is how to define and parametrize “sustainable use.” Promoting forest use that conserves spatial characteristics of forest landscapes and the structure and composition of forest stands was proposed as a way of maintaining elements of biodiversity such as species richness and genetic variation. However, to establish the parameter space for sustainable forest use, it is essential to consider the nutrient requirements of forest systems, that is, plants and animals, the need for fertilizer application, and the effects on biogeochemical cycles, a cornerstone of biological evolution and, thus, biodiversity. The use of forest products is inevitably tied to exporting biomass from those ecosystems because products are used elsewhere, thus changing natural practically steady-state ecosystems to open ones. Continued biomass export results in soil acidification and nutrient removal. Among macronutrients, phosphorus takes a key position, but several others have been shown to be depleted in managed-forest systems. Micronutrients are more crucial for forest-dwelling animals, particularly those nutrients that are only essential to animals. Depletion of their reserves, selenium for instance, through biomass export will not affect plants, and initial subclinical effects on animals are difficult to detect. The generalized effect may be reflected in changing rates of recruitment or disease resistance, and thus ecosystem processes. Forest products and their export reduces soil-nutrient reserves, and slash burning and water runoff further add to cumulative losses of several minerals. Such impacts from forest products need to be addressed, particularly for mammals and their unique needs for several microelements. Biogeochemical cycles disturbed by exporting forest products will affect plants and animals and, therefore, ecosystems and their processes, and these effects need to be incorporated in SFM designs.

Key Words: *biogeochemical cycle; fertilizer; macronutrients; micronutrients; phosphorus; selenium; sustainable forest management*

INTRODUCTION

The synthesis provided by Newton et al. (2009) addresses a complex issue, namely the use of natural resources and, in this case, forest products. The goal is to achieve sustainable forest management (SFM), immediately raising the question of how to define “sustainable use” (e.g., Table 1, Goodland and Daly 1996, Newton and Freyfogle 2005).

Although Newton et al. (2009) do not provide a definition of what constitutes sustainable use, several of their statements indicate explicit goals such as the maintenance of forest biodiversity. They found that current approaches to land use were not sustainable in any of their study areas. This was because of frequent livestock grazing, use of fire, and harvesting of forest products that in turn affected the spatial characteristics of forest landscapes, the structure and composition of forest stands, and elements of biodiversity such as species richness and genetic variation.

To achieve SFM, Newton et al. (2009) propose that harvesting is sustainable if forests are protected

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Table 1. Some selected definitions of “sustainability” in terms of their applications.

Concept Label	Application in Practice
1. sustaining maximum/optimum sustained yield:	maintaining natural renewable resources capital
2. sustaining development:	industrialization, expanding economy
3. sustaining economic growth:	increasing GNP
a. sustaining economic growth:	more matter/energy throughout
b. sustaining economic development:	increasing human satisfaction per unit matter/energy, i.e., increased efficiency
4. substitutability concept of neoclassical economics or technological optimism:	when a natural resource becomes scarce, entrepreneurs will find or invent substitutes
5. carrying capacity for humans:	as the interaction of number of people and living standard
6. sustainability:	sustaining profits based on consumption sustaining rapid economic growth

from threats such as livestock grazing, use of fire, and “unsustainable” harvest of forest products, and if species-specific appropriate silvicultural measures are adopted. Newton et al. (2009) evaluate impacts from forest use according to specific research themes, as per the information they provide in Fig. 2 of their article, based on an analytical framework of several identified ecological processes that they provide in Fig. 1 of their article. I suggest that some major ecological processes have been overlooked and must be included before a parameter space for sustainable use can be defined. Newton et al. (2009) indicate awareness of this but, unfortunately, they only make a short reference to it in Appendix 3, stating that their results represent only a partial contribution toward SFM, and that SFM should also encompass other environmental aspects such as maintenance of soil fertility and water quality. Their paper does not mention the nutrient requirements of the plants and animals in forest systems, the need for fertilizer application, nor effects on biogeochemical cycles. Yet, the dynamic of biogeochemical cycles is a cornerstone of biological evolution and, thus, biodiversity (Moe et al. 2005). The definition proposed by Newton et al. (2009) of “sustainable forest use” is essentially limited to harvests not exceeding annual volume increments, and maintaining the structure and composition of forests so that biodiversity is maintained. In what follows, I examine whether the inevitable disturbance of the mass balance of nutrients can be expected to affect biodiversity as well.

FOREST SUSTAINABILITY

Historically, forest sustainability only referred to the harvesting of annual regrowth. More recently, the term has been broadened to include the maintenance of forest health (Hennig 1988). Comerford et al. (1994) suggest that for forestry, “long-term” should mean three harvest rotations. Morris and Miller (1994) estimate that soil reserves of macroelements will generally be depleted after only several rotations (Table 2). However, sustainability should encompass more than just harvesting the present maximal level of primary or secondary productivity. It must incorporate systems ecology (Myers 1993). Giampietro (1994) uses hierarchal theory to conclude that long-term sustainability has to prioritize the highest system level, the life-supporting ecosystems. Lower-level phenomena such as economic criteria necessarily become secondary in importance to ecologists, but in real life these may be the dominant factors in creating short-term and unsustainable conditions.

I define sustainability as comprising those activities that can be repeated indefinitely within the constraints of the natural fluxes of energy and nutrients that produced a specific ecosystem. For

Table 2. Forest-product harvesting and export of minerals in relation to total pool (over a 35-yr rotation) (Dyck and Cole 1994).

Element	**Nutrient Removal (kg/ha)**	**Max. Removal of Total Pool (%)**
Nitrogen	753	11
Calcium	553	62
Phosphorus	92	7
Magnesium	141	10
Potassium	498	13

forest systems, I propose a time frame of 1000 yrs to determine the criteria needed for defining sustainability. This is based on the time needed for the development of soils permitting forest communities (DeAngelis 1992, Hildebrand 1994).

The current use of forest products is inevitably tied to exporting biomass from those ecosystems, because products are used elsewhere. However, natural ecosystems are characterized by levels of product removal, i.e., nutrient export, that are close to zero by achieving climax or steady-state levels of plant and animal biomass and soil organic matter (Berger et al. 1989, Helyar 1991, DeAngelis 1992, Dobrovolsky 1994). Therefore, it is evident that wood-fiber production, patterns of human distribution, and economic incentives are causing an export of wood products and nutrients from production sites. Although agriculture has long recognized the need for nitrogen (N), phosphorus (P), and potassium (K) as basic plant fertilizers (NPK) to maintain high output rates, there has been little concern for the destiny of other elements. In fact, the implicit assumption is that export of all other elements is not significant for the welfare of plants or animals. However, more recently, fertilizing was also recommended to replenish nutrients according to amounts exported by forest harvesting to reduce detrimental effects on forest productivity (Merino et al. 2005), implicitly referring to nutrients important for trees.

Natural systems typically exhibit biologically important element cycles that are practically closed at local levels (DeAngelis 1992, Dobrovolsky 1994). Evidence from deciduous and coniferous forests that are relatively undisturbed by humans indicates that small net nutrient losses are counterbalanced by weathering or atmospheric depositions (Spurr and Barnes 1980, Kennedy et al. 2002). In contrast, systems disturbed by humans are characteristically open, with large quantities of material being translocated to other areas. Some of the consequences are well accepted in agriculture and also forestry, and remedies to counter the effects of nutrient export are also well established, namely the input of NPK fertilizers (Brady 1990). Hence, biomass export from woodlands raises concerns about the fate of mineral cycles. Aside from the direct removal of elements, additional consequences on mineral cycles stem from changes in soil qualities, including soil acidification (e.g., Flueck 1990). Soil acidification results from the export of biomass that has absorbed base cations while depositing H+ in soils (Helyar 1991, Gustafsson et al. 1993, Moreno and Gallardo 2002). In natural closed systems, most available nutrients are trapped in biomass, and subsequent nutrient loss and associated soil acidification are minimal. Soil quality is typically changed over time periods several times longer than what is required for soil formation, which in central Europe is about 10 000 yrs (Helyar 1991, DeAngelis 1992, Hildebrand 1994, Moreno and Gallardo 2002).

MACROELEMENT CYCLES

Watmough and Dillon (2003) showed that forests in central Ontario, Canada, lost calcium (Ca) and magnesium (Mg) from acidification. The Ca lost in 17 yrs represented up to 60% of the available pool. Calcium depletion from biomass export in southeastern U.S. forests was suggested to reduce soil reserves to less than the requirement for a merchantable forest stand in about 80 yrs, but harvesting results in Ca depletion in most forest systems (Federer et al. 1989, Huntington et al. 2000). Recently, the soil in the Black Forest in Germany was shown to contain <50 kg/ha of exchangeable Mg reserves in the rhizosphere, down to 60 cm. This is approximately the amount in the biomass of growing spruce forests (Hildebrand 1994). Exports of Ca, Mg, K, and especially P in several tree species due to conventional harvesting were similar to or higher than the soil-available reserves (Yanai 1998, Merino et al. 2005). Even when plant-available soil-nutrient reserves become very low, there can still be high growth rates in forests over short periods, i.e., decades. Biomass growth rates are not an indicator of soil nutrient-reserve conditions (Hildebrand 1994). Macroelement deficiency is increasingly recognized in more extensive production systems such as forestry.

Phosphorus

The biogeochemical cycle of P in terrestrial systems currently takes a key position because of the global scale of human-induced alterations in its dynamics. These alterations have basically turned the cycle into a predominantly open one (Abelson 1999, Smil 2000). The importance of this stems from our reliance on production systems to channel organic material into far-removed centers of human consumption, mainly in the form of food, fiber, wood products, and fuel. Production systems based on forestry, animal husbandry, and agriculture all rely on local P reserves in soil, but in all systems, the continued import of P is necessary. This has been first and most notoriously recognized in agriculture (Ingerslev 1998, Yanai 1998, Bennet et al. 2001, Wivstad et al. 2005). The current emphasis on increasing the production of biofuels through forestry in response to the energy crisis represents an additional enormous demand for P fertilizer, resulting in competition with the food-production system. Areas exploited through extensive production, including range lands, silvicultural systems, and silvopastorial systems, are also important, because they often support wildlife and other biodiversity. Phosphorus is highly vulnerable to loss from biomass export (Dobrovolsky 1994). Thus, depleting soil P reserves not only affects the economy of extensive production systems, but also affects wildlife and ecosystem processes.

For example, extensive cattle production on range lands in San Luis, Argentina, removed 0.3 kg/ha/yr of P, a level considered unsustainable if not accompanied by fertilizer application(Veneciano and Lartigue 2001, Veneciano and Frigerio 2002). Studies of forests throughout the U.S. have indicated that the harvest of only logs removed 0.08–1.02 kg/ha/yr of P, whereas whole-tree harvest removed 0.24–1.75 kg/ha/yr of P. These harvested, but unfertilized, systems lost P regardless of harvest intensity and were considered unsustainable (Mann et al. 1988). Whole-tree harvest in other forests removed 20–50 kg/ha/yr, or half, if only the logs were removed (Federer et al. 1989). Heilman and Norby (1998) reported on forest harvesting that required a fertilizer input of 151.75 kg/ha/yr of P to compensate for exports.

Newton et al. (2009) did not mention P, yet other studies in the same area showed that the available P pools were roughly equivalent to the P found in the biomass of pristine forests in Patagonia, Chile, and that the annual P requirement was <3 kg/ha in growing conifer and mixed forests (Thomas et al. 1999). Concern was expressed that whole-tree harvest would thus remove a large portion of the accumulated P reserve in these forests (Peri et al. 2008).

MICROELEMENT CYCLES

Forest landscapes, and especially those found in mountain ranges, are often naturally low in macro- and micronutrients (Kubota et al. 1967, Kubota and Allaway 1972). A lack of any of the essential elements can be limiting to biological production, and they are particularly important in the more heterogeneous terrestrial systems (DeAngelis 1992, Dobrovolsky 1994).

Microelements Essential for Plants and Animals

Many trace elements are essential to both plants and animals. Although plants may be partially affected by a deficiency, they may still grow, but they will provide inadequate forage to herbivores. Many regions that are characterized by low concentrations of soil and plant trace elements thus induce subclinical or clinical deficiencies in mammalian herbivores. When such areas are exploited, even moderately, these microelements may become important deficiencies in animal diets. For instance, copper (Cu) and molybdenum (Mo) contents in plants are generally associated with soil availability. The Cu requirement of plants is important, but it is much lower than that of animals (van Soest 1982, Jones and Wilson 1987). As forest landscapes are modified, secondary Cu deficiency can appear in wild herbivores (Alloway and Tills 1984, Bonniwell 1986). The apparently new Alvsborgs disease was discovered in Swedish moose (*Alces alces*) in 1985, resulting in >1000 deaths over a 9-yr period (Steen et al. 1989, Broman et al. 2002). Many animals showed severe Cu deficiency, and some were diagnosed as suffering from primary Cu deficiency (Rehbinder and Petersson 1994). Furthermore, between 1982–1988, a decrease of about 30% in hepatic Cu concentration was observed, and by 1994 it had dropped by 60% (Frank et al. 1994, Frank 1998). In the same time period, Mo levels in moose increased 20%–40%, which was probably related to an increase in the pH of the soil and water from liming undertaken to counteract acidification in this region (Frank 1998, Frank et al. 2000). In general, weathering does not keep pace with the documented losses of several macro- and microelements due to increased soil acidification in southern Sweden (Bergkvist et al. 1989). For example, the present-day extractable soil pool of zinc (Zn) in the deciduous and coniferous forests of southern Sweden is only 50% of the level it was 40–50 yrs ago.

Microelements Affecting Only Mammals

Elements not essential to autotrophs but essential to heterotrophs, represent an additional complexity of nutrient-cycling dynamics. In these cases, disturbance to mineral cycling will only affect the heterotrophs, although the consequences will have cascading effects throughout the ecosystem. Even though livestock can be treated for nutrient imbalances, practical protocols are not available for wildlife species.

Significant areas worldwide have marginal soils relative to certain microelements (Kubota et al. 1967, Kubota and Allaway 1972), resulting in subclinical deficiencies that are mostly unrecognized in wildlife (Flueck 1994) or in extensive animal-production systems (Johnson et al. 1979, Jones et al. 1987). However, the incidence of overt and subclinical deficiencies is likely to increase where biomass export is accelerated.

For example, selenium (Se), a microelement usually occurring in low soil concentrations, is insufficient for mammals in many areas such as northern Europe, western USA, New Zealand, and China (Kubota et al. 1967, Robinson 1988, Singh 1991, Tan and Huang 1991). It is also known to be deficient in the Andes of Chile and Argentina (Wittwer et al. 2002, Contreras et al. 2005, Vivanco et al. 2006). Selenium is nonessential to plants, but occurs in plants proportional to soil concentrations. Selenium is an essential microelement for mammals and it is important at very basic biochemical levels. Selenium deficiency affects juveniles, resulting in increased mortality during the neonatal period (Keen and Graham 1989). Because of these basic functions, suboptimal Se levels result in a myriad of symptoms, and pronounced deficiency is lethal. With regard to wildlife, forestry sustainability implies maintaining functional geochemical and biogeochemical cycling of Se. Several factors make the Se cycle susceptible to depletion with its associated consequences for fauna (Flueck 1990, Flueck and Smith-Flueck 1990). The acidification of soils transforms Se into unusable forms, i.e., forms that are unavailable for plant uptake (Geering et al. 1968, Mikkelsen et al. 1989). For example, soils in southern Swedish forests showed a tenfold increase of proton concentration throughout the soil profile over a 25–40-yr period (Gustafsson et al. 1993). A 20-fold increase occurred in Germany over a 65-yr period (Hildebrand 1994), both of which impacted Se absorption.

Thus, there are several aspects of biomass removal that need special consideration. First, the characteristics of the Se biogeochemical cycle result in most of the Se available to organisms to be accumulated in biomass (Gissel-Nielsen and Hamdy 1977, Swaine 1978). Consequently, the export of plant biomass, whether directly or indirectly as through herbivores, removes important proportions of bioavailable Se. Second, plant export results in soil acidification that decreases Se absorption rates by plants (Helyar 1991, Gustafsson et al. 1993). Third, biomass export in the form of ruminant herbivores not only removes Se, but Se deposited in feces and urine is principally in forms unavailable to plants (Butler and Peterson 1963, Peterson and Spedding 1963, Olson et al. 1976). Fourth, Se removal by volatilization during fires may be substantial in systems with marginal or low Se concentrations because much of the Se available to plants occurs in standing biomass (Swaine 1978, Frost 1987). In addition, other anthropogenic activities strongly decrease bioavailability of Se through immission and mobilization in acidified soils and, notably, an increased concentration of heavy metals renders Se unavailable to plants. Furthermore, exposing animals to heavy metals increases their physiological need for Se, as do other oxidative stresses involving exposure to pollutants or toxicants. Thus, these factors have to be accounted for in a discussion of Se requirements. These circumstances help to explain the worldwide increase in incidence of Se-responsive diseases (Jenkins and Hidiroglou 1972, Gissel-Nielsen 1975, Fischer 1982, Millar 1983). Programs of fertilizing soils with Se to overcome deficiencies have demonstrated that applications last only 1–2 yrs (Gupta et al. 1982, Watkinson 1987). Thus, effective fertilizing programs at the landscape level would be prohibitively expensive.

DISCUSSION

The continuous export of wood products based mainly on forest-regrowth rates as a surrogate for sustainability ignores other relationships that are important for the healthy functioning of forest ecosystems. Because of the constraints of mineral-cycle dynamics, traditionally managed forests may not be sustainable for wood production in the long term, and may be even less sustainable for forest-dependent animals. As pristine forest systems are practically closed with respect to nutrient flows, even moderately exploited forests have been shown to diminish certain mineral reserves.

As ecosystems mature, many nutrients become primarily recycled internally, and the pool of such nutrients stored in biomass becomes larger as the nutrient pool in soil becomes increasingly reduced compared with the biomass (Odum 1991, DeAngelis 1992, Yanai 1992, Ballantyne et al. 2008). In fact, the release of such nutrients from the weathering of rock is insignificant in relation to what the maximal standing biomass needs and, thus, mature forest systems may take thousands of years to develop through efficient biogeochemical cycling with increasing nutrient accumulation (DeAngelis 1992, Yanai 1992, Hedin et al. 1995, Chadwick et al. 1999).

The Importance of the Macronutrient P

Phosporus is a rather immobile element that, in absence of harvesting, results in nearly closed local cycles and is often a limiting factor (Woodmansee and Duncan 1980, Smil 2000, Gillooly et al. 2005). The concentration factor for soil–plant systems is possibly the highest known (Asimov 1962). 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 (Smil 2000). As natural input and output rates are minimal, developing systems slowly accumulate P until a steady state is reached and biological recycling is maximal at both the organism and ecosystem levels (Federer et al. 1989, Yanai 1992, Chadwick et al. 1999, Ballantyne et al. 2008). This secondary cycling of organic P has a rapid turnover time 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 (Smil 2000).

Productive systems involving the harvest of crops, trees, and animals have all been recognized to remove more P than occurs under natural conditions and in excess of the limited inputs, depleting reserves in the process and thus making the system unsustainable. For this reason, P has been termed “life’s bottleneck” by Asimov (1962), a fact published in *Nature* earlier in 1942 (Armstrong 1942, Newman 1997, Chadwick et al. 1999). As extensive production systems not receiving P fertilizer have been shown to become depleted over time (Díaz-Zorita 2002, Jewell et al. 2007), I posit that the land use as described by Newton et al. (2009) is also unsustainable in terms of P.

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, and particularly mammals, or needed at higher concentrations by animals (Flueck and Smith-Flueck 2006). On the other hand, elements like P can serve as an an indication to estimate fluxes of other elements (Flueck 2009). Several microelements essential for both plants and animals are needed at lesser availability by plants. Plant performance then masks an ongoing depletion process that can be affecting animals. Some additional microelements are only essential for animals with no effect on plant performance. Unfortunately, deficiencies of microelements at subclinical levels are difficult to detect, yet their effect on ecosystem processes may be large. Examples of subclinical effects include a reduction in recruitment rates or diminishing resistance to pathogens (Flueck 1994).

Wood production and export remove minerals contained in biomass and thereby reduces soil reserves, and also cause cumulative loss of several minerals through burning slash and water runoff. Such impacts need to be addressed, particularly considering some mammals' unique needs for several microelements. Biogeochemical cycles disturbed from exporting forest products will affect plants and animals and, therefore, ecosystems and their processes. For these reasons, I suggest that mass balances of macro- and micronutrients need to be incorporated in designing SFM.

Responses to this article can be read online at: *http://www.ecologyandsociety.org/vol14/iss2/resp4/responses/*

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