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Biodiversity conservation under energy limitation: Possible consequences of human productivity appropriation for species richness, ecosystem functioning, and food production

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ABSTRACT

The human population appropriates about one-third of global aboveground terrestrial productivity. Although we have only a limited knowledge of the consequences of this effect, it is probable that the decreasing energy available for natural ecosystems will lead to the decrease of biological diversity, ultimately leading to the loss of functioning of natural systems. Such a loss may potentially severely affect also human production systems, since they are inevitably tightly interlinked with natural systems, exemplified by soil communities. This impedes the potential for biodiversity conservation as well as the sustainability of ecosystem services necessary for maintaining human population, and calls for a new research agenda and urgent policy measures.

1. Introduction

While the fact that human appropriation of net terrestrial productivity has reached about one-third of the total above ground production on Earth has been repeatedly acknowledged (Vitousek et al. 1986; Wright, 1990; Rojstaczer et al., 2001, Haberl et al., 2007), its consequences have remained elusive. Intuitively, if Earth's total productivity is roughly constant (Running, 2012), and a part of the energy available to Earth's global system is removed by one species, all the organisms except the "winner" are expected to lose. However, it is not that clear what exactly the global ecosystem loses by this assymetric appropriation of available energy. Although this effect may actually be stronger than any other consequence of increasing human population and activity, so far we do not understand it well. It has been repeatedly argued that increasing pressure of human population on ecosystems leads to the depletion of resources and diversity loss (e.g. Pimm, 2001) and that biodiversity loss can negatively affect ecosystem functioning and ecosystem services (Loreau et al., 2001). However, here we go beyond these straightforward cause-effect arguments. We contend that all these effects are actually tightly linked to each other, potentially forming a positive feedback loop which may in consequence affect both natural and human production systems, leading to far-reaching regime shifts. Moreover, we argue that both the problem and its potential solution do not lie in ecosystem production itself (and the portion which is appropriated by human population) but rather in the way how is energy utilized and dissipated.

Some level of available energy and ecosystem production is clearly needed for maintaining diverse and functioning ecosystems. Although diversity has been thought to reach highest levels in intermediate productivity levels (Rosenzweig, 1995, Huston and Wolverton, 2015), recent findings show that species richness on Earth's surface generally increases with energy availability (Waide et al., 1999; Storch, 2012; Gillman et al., 2015), indicating that lower energy availability necessarily leads to lower species richness. The most straightforward explanation of this relationship is the more-individuals hypothesis (Gaston, 2000) which states that higher energy availability leads to a higher total number of individuals, which can be then divided into more species with viable

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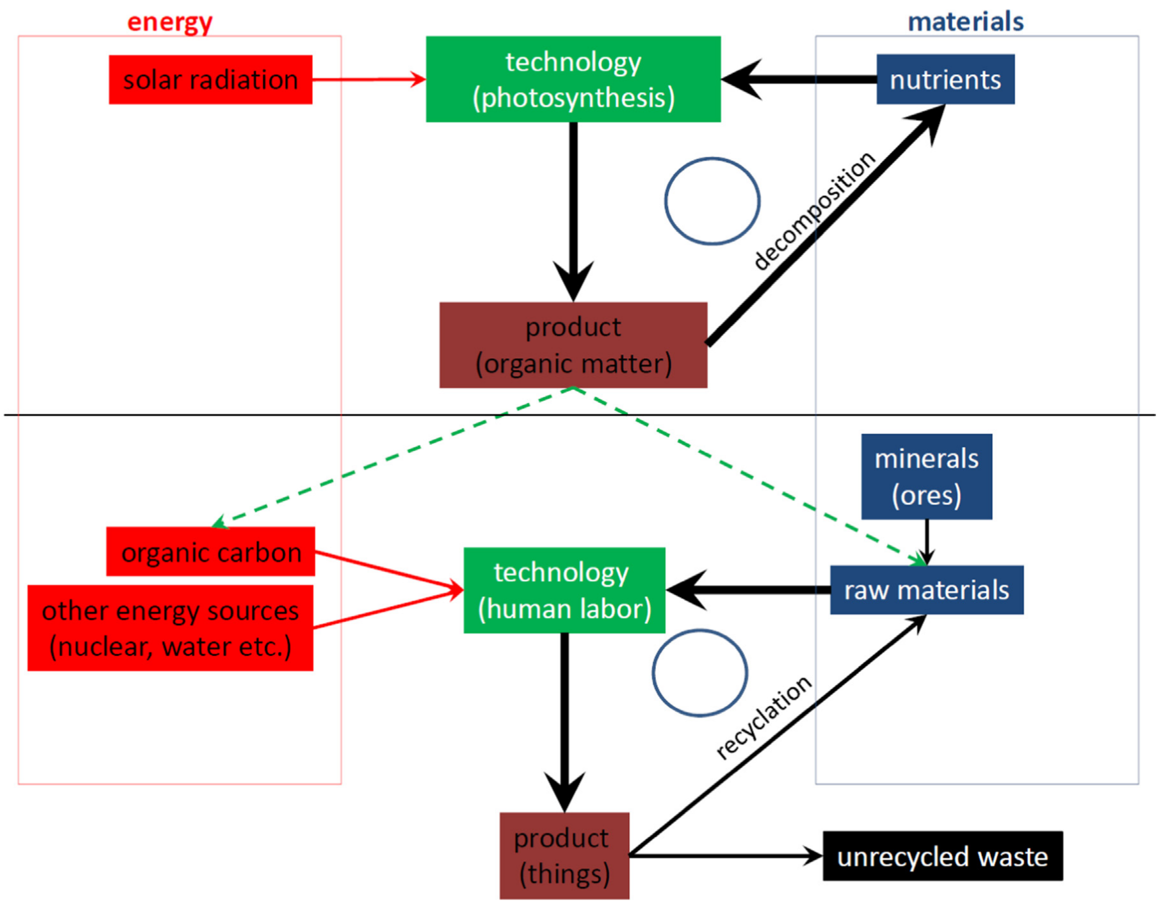

Fig. 1. Analogies and interconnections between natural (above) and human (below) production systems. Both the systems use materials and energy to make products through "technology", and have the ability to recycle materials. However, while natural ecosystems are extremely effective in recycling, human production systems are rather ineffective, and they rely on technological innovations to maintain production. Natural systems provide both materials and energy for human systems (green dashed arrows), although the transfer of energy from natural systems to human systems may take a long time if human systems use fossilized organic carbon. While energy is not extracted from recent production cycles of ecosystems in the case of fossil fuels, in biofuels it is extracted. Extraction of energy and materials from natural cycles affects their functioning (including effective recycling), ultimately compromising their ability to provide goods and services for human population. Sustainable production of both systems is therefore crucially dependent on the maintenance of the natural production cycle. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

populations. This theory has some problems (Currie et al., 2004), and direct causal links between energy, total number of individuals, and number of species are unclear (Storch, 2012). Still, there is mounting evidence that biological diversity is constrained by available energy (Hawkins et al., 2003, Haberl et al., 2005). We can thus expect biodiversity loss due to human appropriation of productivity regardless of exact causality, even without assuming any specific loss of habitats, hunting, pollution or other known biodiversity threats. It is even possible that this effect lies behind the more proximate reasons of diversity loss as an ultimate cause of biodiversity crisis. Therefore, we should ask to what extent are we able to cope with biodiversity loss and protect nature, given that there will be not enough energy for sustaining high diversity levels on Earth.

1.1. The consequences of human appropriation of NPP

Human appropriation of NPP includes food consumption (including food for livestock), and paper, wood and fiber production (Haberl et al., 2007). Part of its effects thus comprises simple habitat transformation, with consequent shrinkage of natural habitable area for wild plant and animals, fragmentation of their populations and eventual local or regional species extinction. However, this effect of habitat loss on diversity loss is not the only consequence of human NPP appropriation. Although not all diversity is lost within intensively cultivated areas (Pereira and Daily, 2006), these areas are considerably depauperated due to the pressure on the economic profit from all the crop and consequent simplification of all ecosystem functioning towards rapid growth of a small set of economically valuable primary producers. Additionally, most of the biomass is removed, so that the energy it contains is not allowed to participate in further chains of energy flow and matter conversion within the ecosystem. This may compromise other ecosystem functions and services due to the local decrease of diversity (Loreau et al., 2002) and/or abundance of common species which provide important ecosystem services (Inger et al., 2015).

There are situations in which we can imagine such an effect quite easily. Soil ecosystems, for instance, take their energy from dead organic matter, and soil fauna is generally less abundant in habitats exploited by man (e.g. Crossley et al., 1992). This effect has been traditionally explained as a result of disturbance (see Müller et al., 2014) or use of pesticides or mineral fertilizers, but all these effects are ultimately driven by the redirection of energy flow by human activities with the aim to appropriate maximum of the biomass production from ecosystems (Meehan, 2006). Soil microorganisms and soil fauna contribute significantly to the creation and maintenance of soil structure (Anderson, 1995; Setälä, 2002), so that persistence of soil organic matter is rather a property of the ecosystem than a simple by-product of chemical/

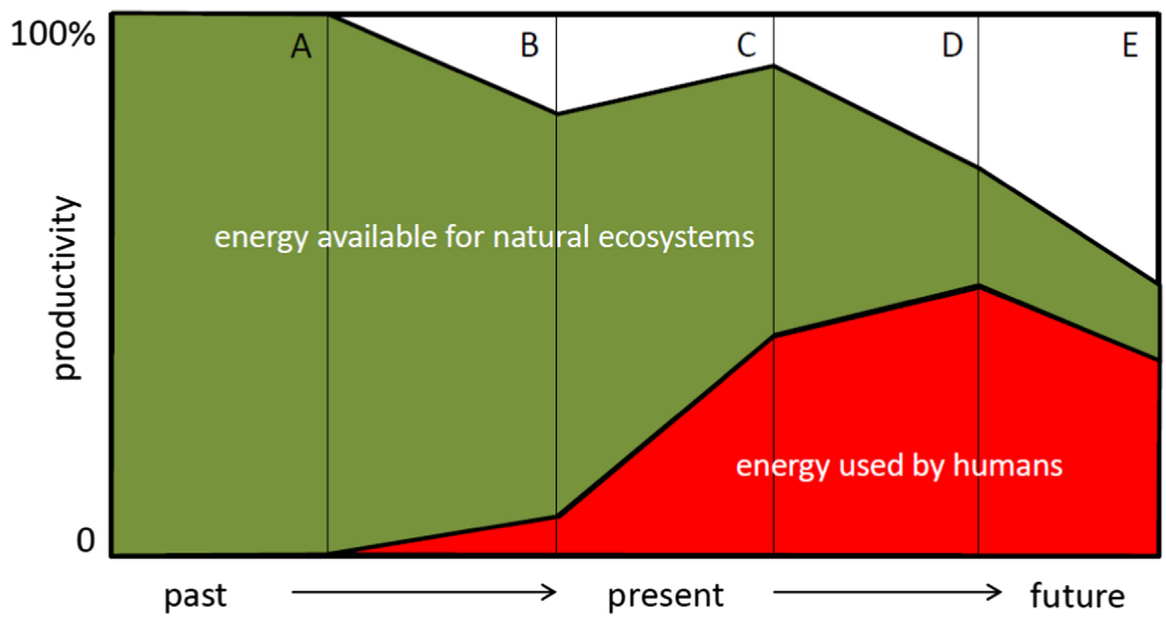

Fig. 2. Conceptual model of productivity changes associated with the development of agriculture. The green color represents the production of natural systems, the red color is the production of agricultural systems appropriated by humans (HANPP). The original landscape (A) has been deforested and transformed into fields, decreasing total productivity, as agricultural systems do not reach productivity levels as high as natural ones (B). The intensification of agriculture associated with using fertilizer (C) massively increases agricultural production, and thus (potentially) also the total production of the landscape. However, such intensification leads to compromising ecosystem functions due to lower energy availability for organisms in natural systems, so that further increase of agricultural production is slower and total production of the landscape may decrease (D). Eventually, degraded ecosystem functions may be insufficient to maintain this level of agricultural production, and both agricultural production and total production decrease (E). To avoid this scenario, it is necessary to minimize losses of natural production (green area) in order to retain ecosystem functions which are vital for maintaining both agricultural and total production of the landscape. This can be attained by keeping some proportion of the land as extensive farmland and natural ecosystem (space for nature), and calls for close monitoring of not only agricultural, but overall production levels at an appropriate scale, ie. developing appropriate policy instruments including the necessary science input. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

molecular structure of it (Schmidt et al., 2011; Fierer et al., 2013). Structural impoverishment of the soil and the decrease of soil organism abundance in intensive agriculture can thus promote each other via positive feedback. Lower abundance of soil organisms linked with simplification of soil communities (Crossley et al., 1992; Bedano et al., 2006) can ultimately lead, despite high functional redundancy of soil microorganisms (Griffiths et al., 2000; Setälä and McLean, 2004), to disappearance of some functional groups of soil organisms. This may lead to the decrease of the ability of soil to recycle and/or keep nutrients necessary for plant production, including food production for human population. The high level and ever growing extent of soil degradation is already recognized as an important threat to both biodiversity and agriculture (European Commission, 2006), demanding a policy response (Montanarella and Vargas, 2012; Kibblewhite et al., 2012).

1.2. Links between natural and human-made systems

The relationship between energy availability, diversity and abundance of organisms, and ecosystem functioning necessarily extends into ecosystem services for human population, since natural and human-made production systems are tightly interlinked (Fig. 1). They both use raw materials and transform energy using what we can generally call “technology”. In natural systems, virtually all energy comes from solar radiation, but only a tiny fraction of it is utilized due to the relative inefficiency of photosynthesis. While the energy source is therefore virtually unlimited, “technology” comprising photosynthetic apparatus is the limiting factor, although some raw materials (nutrients) can be limiting as well. In contrast, technology is the least rigid element in human systems due to human ability to develop innovations. Still, the major source of energy for human systems is actually dead organic matter (either recent or fossilized), i.e. again a product of photosynthesis. Both the systems are thus ultimately limited by photosynthetic efficiency and raw material (e.g. nutrient) availability. Although human systems may obtain energy from completely different sources (e.g. nuclear fission), food production systems are necessarily linked with natural systems, and will remain dependent on them.

In such a situation, it is questionable to what extent we will be able to further intensify agricultural production and maintain it. The above-mentioned example of soils suggests that human appropriation of Earth’s productivity can potentially lead to impoverishment of ecosystems with consequent loss of functions necessary for maintaining food production (Fig. 2). Such loss of function can be partially overcome with increasing energy and fertilizer input, but this cannot go beyond certain limits. Availability of resources (e.g. phosphates or water) and the price of energy may compromise agriculture profitability. This may lead to pressure to abandon some of the measures related to environmental protection and food safety applied in agriculture today, creating a potential positive feedback further aggravating the problems. In other words, we will be hardly able to pay the ecosystem services debt we are now creating without compromising our living standards.

1.3. Ways forward

These considerations set an urgent policy agenda. Although demands of human population will hardly allow significant lowering of human appropriation of ecosystem production, there are some ways in which the effects mentioned above could be mitigated. Most importantly, the energy appropriated by humans may not necessarily be entirely lost from the system. Natural systems are characterized by continuous flow of energy and effective recycling of "waste", so that even large amounts of consumed production (e.g. by large herbivores) represent an energy which is further dissipated and used step-by-step by multiple organisms, fueling the diversity and functioning of ecosystems. In contrast, the energy appropriated by humans has been mostly utilized in large steps, and the vast majority is rapidly converted to heat. This is also a major problem with the bio-energy concept, based on direct use of biomass without allowing energy to dissipate back step by step - plants used for bio-fuels do not participate in complex chains of energy flow and matter conversion which is necessary for maintaining ecosystem diversity and functioning. To maintain it, it is necessary to leave at least some portion of energy to natural systems, either within areas which are not used for production and which may serve as a source of species or functional groups necessary for all ecosystem services, or within cultivated areas themselves. The amount of energy necessary for ecosystem functioning that would avoid collapses or substantial conversions remains to be estimated.

Since organisms have evolved so that they have optimized their performance, it is reasonable to assume that natural ecosystems reach maximum productivity under given conditions (Roy et al., 2001). Intensive agricultural systems can achieve similar productivity levels only with high external input of energy and nutrients. It is thus also crucial to preserve natural systems which can provide functions that are not provided by intensive agricultural systems, and which keep up high levels of terrestrial productivity. This may go beyond the simple notion of ecosystem services with their particular function: we contend that maintaining natural systems is essential for sustaining energy input into the biosphere which can be further utilized for various functions, including those essential for food production (pollinators represent a classical example).

Energetic impoverishment of natural ecosystems on Earth asks for a new research agenda. It is urgent to explore the links between energy availability, species as well as functional diversity, and ecosystem functioning, to reveal the conditions under which there is a chance to maintain biodiversity as well as vital functions for sustainable food production. So far, we have for instance very limited knowledge of what is happening under the soil surface, and what we should expect under different scenarios of future development. Since all these changes will be necessarily linked with economic changes (price of energy and food, availability of fertilizers etc.), there is an urgent need to develop models and approaches which will be dealing with the interface of ecology and economy. These two fields are – and will be – much more tightly connected under the situation in which further growth is inevitably limited (Brown, 2011), and this interface thus represents a major challenge in this millennium.

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