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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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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

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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.

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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/

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