

Opinion

Deciphering the Biodiversity-Production Mutualism in the Global Food Security Debate

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Without changes in consumption, along with sharp reductions in food waste and postharvest losses, agricultural production must grow to meet future food demands. The variety of concepts and policies relating to yield increases fail to integrate an important constituent of production and human nutrition – biodiversity. We develop an analytical framework to unpack this biodiversity-production mutualism (BPM), which bridges the research fields of ecology and agroeconomics and makes the trade-off between food security and protection of biodiversity explicit. By applying the framework, the incorporation of agroecological principles in global food systems are quantifiable, informed assessments of green total factor productivity (TFP) are supported, and possible lock-ins of the global food system through overintensification and associated biodiversity loss can be avoided.

Consequences of Increasing Food Production

The quest for greater crop output for food and non-food products [1–3] leads to both an increase in agricultural land use and an increase in yields, typically achieved through an intensification of cultivation methods that help to **close yield gaps** (see Glossary) [4,5,62]. This, in turn, leads to a loss of biodiversity in agricultural landscapes [7] and increases pressure on natural diversity [8], which continues declining despite ongoing efforts for protection [9]. The avoidance of food waste and dietary changes offer two demand-side options to reduce pressure on food production [10], but these have thus far not been achieved at the macro level [11].

Biodiversity is a crucial component of ecosystem functions that are essential for agricultural production, such as soil fertility, pollination, and biocontrol (i.e., the control of plant pests by their natural enemies) [12–15]. This interdependence of biodiversity and agricultural production has led to a variety of concepts that aim to optimize the management of agricultural landscapes, balancing yields, biodiversity, and sustainability [16]. These concepts make use of **agroecological principles** [17], promote **organic farming** [18] suggest **ecological intensification** [19], or **sustainable intensification** (SI) [20], compare **land sharing** and **land sparing** concepts [21–23] and take the perspective of managing a coupled socioecological system (SES). While there is much published research on the SES concept, quantitative, empirically-based, and model-based implementations are largely lacking or their improvement through process-based validation is pending [24]. As a result, it is currently not possible to capture and quantify the biodiversity-production mutualism (BPM) in its entirety. However, recent research provides the necessary basis for such a comprehensive, quantitative, process-based understanding of the BPM concept [15,24,25].

A Multidisciplinary Perspective on the Relationship between Agriculture and Biodiversity

How is Biodiversity Affected by Cropland Management?

Management of agricultural landscapes serves the provisioning of agricultural goods and has had mostly negative impacts on biodiversity [7,8]. This occurs through both the expansion and

Highlights

Increasing demands for agricultural commodities are resulting in more intensely managed landscapes. This is at odds with biodiversity conservation and largely ignores farmland biodiversity's supporting function for high and stable yields.

An overhaul of agroeconomic models to account for the biodiversity-production mutualism is urgently needed to answer a question of utmost importance: How do we manage the resources of our planet in such a way that we produce enough healthy food without destroying our life-support system?

A comprehensive analytical framework is provided that accounts for multitrophic biodiversity-production processes; bridges disciplinary boundaries between agronomy, agroecology, economics, and conservation science; and elucidates the strong interactions of ecosystem functioning with food security and maloutrition.

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intensification of cultivated areas, which in turn warps the composition of landscapes and their structure. Conventional intensification to increase yields is typically done by homogenizing the landscape (fewer, larger fields), increasing inputs (labor, fertilizer, irrigation, chemicals), and/or augmenting harvest intensities [26-29]. Conventional intensification typically leads to a loss of species present and a change in the composition of communities, for example, in the form of a general decrease in abundance [7,8,18]. There is evidence of a long-term decline in insect species due to habitat loss and agricultural intensification [30,31]. This can also be associated with a proportionally greater abundance of pest species due to a reduction in biological pest control [32]. Ecological intensification directly or indirectly addresses that trade-off [19,33]; however, a process-based understanding of these relationships is context-dependent and, therefore, highly fragmented [34,35]. Homogenization of environmental conditions typically leaves a few abundant generalists, while specialists tend to be lost [24,36]. Pests and their predators react differently to the composition of the surrounding landscapes [15]. Consequently, predicting the effects of intensification requires careful consideration of multiple factors, including landscape configuration and species characteristics [25,37,38]. This requires a broader perspective that includes management of landscapes.

Comprehensively Measuring Agricultural Sustainability: Green Total Factor Productivity

The positive effect of intensifying land management on yields is well studied. The relevant range of classical reductionist production functions is regarded as positively sloped in input intensification, as no rational agent would purchase inputs to reduce production (Figure 1A). However, groups of farmers operating in interlinked agricultural landscapes may find that their individual choices collectively reduce productivity because each operator ignores the mutualism of biodiversity and production (Figure 4.1 in [39]). Hence, the yield function in intensification may become flat or even turn negatively sloped when BPM is considered (Figure 1B). This suggests a revision to agroeconomic models. In standard models, each input is usually weighted according to its economic contribution, and an index of all outputs can be obtained by weighting each crop according to its share in the total economic value. If the output index increases faster than the input index, total factor productivity (TFP) increases [40]. TFP was proposed to provide a metric for agricultural sustainability [41,42], but since the output and input measures typically cover only those aspects for which markets exist, nonmarket implications are ignored [43].

TFP growth can be neutral or beneficial to biodiversity. For example, pest- or disease-resistant varieties can achieve the same yields with reduced use of potentially harmful chemicals. Here, the technology can have positive external effects (e.g., improved health or reduced chemical runoff) [44]. However, new technologies are not always environmentally friendly. For example, the use of the dicamba weed killer in conjunction with new soybean varieties has led to numerous lawsuits from people who suffered collateral damage from drifting dicamba [45]. These negative results due to the new technology would be ignored in traditional TFP approaches but would be captured by a green TFP approach – also termed total resource productivity (TRP) [43]. Green TFP or TRP include negative outputs (such as pollution or biodiversity loss) and inputs based on natural resources (such as groundwater or biodiversity) valued for their societal contribution rather than at their (often lower or zero) market value. Green TFP has been suggested as a more appropriate performance measure. However, attempts at operationalization have frequently failed [39], partly due to missing indicators but also due to a lack of available modeling concepts. Applying the BPM concept can inform estimates of green TFP [46].

A landscape-related perspective that incorporates BPM has rarely been brought to bear in production agriculture, for at least two reasons. First, the missing indicators problem - valuation of nonmarket inputs and outputs - is challenging because the details of the BPM relationship are complex and location specific. Second, relatively few individual farms operate at the scale where

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Agroecological principles: are supposed to contribute to transforming food systems by applying ecological principles (ecological intensification) to ensure a regenerative use of natural resources while addressing the need for socially equitable food systems. While the focus initially was on understanding field-level farming practices, now landscape-scale processes (such as BPM) as well as the development of equitable and sustainable food systems are considered [17].

Closing yield gaps: aims at assessing differences between observed yields and those attainable under comparable bioclimatic conditions. Differences are identified by either statistical or modelbased comparisons to similar regions [4,5,62]. Critiques: (i) such comparisons cannot account for socioeconomic constraints (prices for inputs and outputs: access to markets, credit, and technology) and ignore impacts on ecosystems and biodiversity; and (ii) nutritional values are considered implicit, 'hidden hunger', that is, lack of micronutrients, unaddressed.

Ecological intensification: entails the replacement of anthropogenic inputs or enhancement of crop productivity through fostering biodiversity-based ecological functions in agricultural practices [19]. Recent research tends to focus on specific processes (e.g., pollination) rather than outcomes (e.g., profits) and results are presented at spatiotemporal scales that are less relevant to farmers [33].

Land sharing: less intense, wildlife friendly farming at the cost of further agricultural expansion [6]. Critiques: (i) studies adopt a regional, rather than a global perspective [21]; (ii) its scale dependency hampers a clear association of landscapes to sharing or sparing type [22]; and (iii) the sparing concept suggests to preserve biodiversity at distant sites while compromising biodiversity in farmlands, which maintains ecosystem functions such as biocontrol or pollination (BPM

Land sparing: an increase of set aside land for biodiversity protection while increasing production (mostly through intensification) on the remaining managed land.

Organic farming: characterizes farm management that focuses on wildlife friendly farming by avoiding the use of



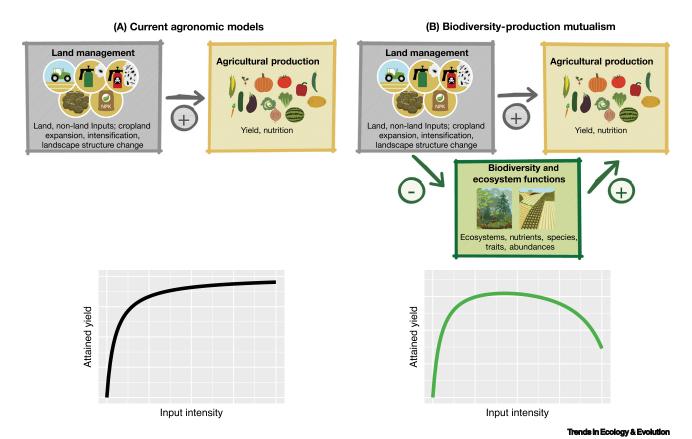


Figure 1. Conceptual Juxtaposition of Current Agronomic Models (A) and the Biodiversity-Production Mutualism (BPM) Concept (B). In both cases, panels (A) and (B), landscape management for agriculture with all its aspects (gray box) impacts production positively (gray arrow). The relationship between input intensity levels and yields can be assumed as a saturation function [lower part of panel (A)]. The BPM concept, panel (B), specifically considers positive effects of biodiversity and ecosystem functions on yields, but also negative effects of land management on biodiversity-based ecosystem functions. In the BPM concept, however, a humpback-shaped curve can be expected due to declining yields at very high levels of input intensity.

taking a landscape-related perspective results in private gains to the owner/operator of the farm. As shown in Figure 1, recognizing the BPM concept opens the possibility that, for intensively operated land, biodiversity gain may coincide with minor yield losses; or, for extensively operated land, substantial yield gain can occur with limited intensification if biodiversity, and hence the BPM relationship, is maintained. Indeed, gains along both dimensions may be possible [47], for instance, with positive effects of intercropping, as shown in a recent global-scale meta-analysis [48].

Rethinking the BPM in Agroeconomic Models Modeling the BPM

To implement and test the BPM concept, substantially revised agroecological models and their implementation in an analytical framework are required. Box 1 illustrates how the mutual feedbacks between biodiversity and production can be integrated into regional or global agroeconomic models. The starting point is the simulation of plant production for a given location depending on the environmental conditions and the inputs for agriculture. In order to make these simulations dependent on ecological functions and incorporate multitrophic interactions, suitable scaling parameters are required that consider landscape structure and composition. Homogeneous spatial units providing the input parameters for yield simulations are usually derived from spatially referenced intersection data on environmental conditions. For the analytical synthetic pesticides, usually with expected lower yields or profits [18], that is, a specific farm level application of agroecological principles and ecological intensification. Critiques: (i) there is no explicit use of biodiversity, which would require landscape-scale management beyond farm level [23] and (ii) certification schemes vary across regions and countries.

Sustainable intensification (SI): is closely related to agroecological principles but suggests a multifaceted approach and oversees the entire food system by considering nutrition, food sovereignty, and adaptation to localities defined by socioeconomic as well as environmental conditions. SI encompasses four aspects: (i) attain higher yields, while (ii) achieving a major reduction in environmental impacts. (iii) achieve a drastic reduction in resource intensive foods (change diet gap), and



Box 1. Analytic Framework Deciphering the BPM

An agro-ecological and -economic framework that comprehensively accounts for the most relevant land and non-land inputs, including biodiversity, starts with underlying crop growth processes. Figure IA illustrates how growth of individual crops depends on environmental parameters E, such as available water, nutrients, and soil fertility, but also anthropogenic inputs, such as labor, irrigation, and fertilizer. This is illustrated by a differential equation estimating crop growth Y dynamically. Crop growth could be implemented in more complex ways, that is, by distinguishing different plant organs, or in more aggregated ways, such as using regression models that do not account for intra-annual dynamics. To upscale such models to larger regions or even to the global level, such models are often repeatedly run with changing model parameters depending on the location x and by using spatial maps that supply data on cropland extent, environmental conditions E, and anthropogenic input A (Figure IC).

Incorporating multitrophic interactions of crop growth with aboveground biodiversity in such an approach is challenging, as biodiversity changes are driven beyond the point scale. A crop growth model that fully accounts for the BPM requires incorporating landscape-scale properties, which are the relevant drivers of biodiversity, such as composition and configuration of the landscape as well as input intensity [63]. While information on input intensity L_I is often available on a grid scale, such as fertilizer F, irrigation I, or labor L, the quantification of landscape composition and structure can be assessed by landscape metrics (e.g., [52]). A specific multitrophic interaction (e.g., pollination, biocontrol) defines the radius around a field in which landscape configuration, composition, as well as input intensity matters for the relevant biodiversity metrics (BD), such as presence, absence, or abundance of important species traits that provide pollination or biocontrol services. For example, insect-based pollination landscape metrics can be calculated for a radius of 250 m, 750 m, or 1 km around fields, distances of up to 3 km can be relevant for both pollination and biocontrol-providing organisms [64-66].

Biodiversity data on species' presence or abundance in turn alters the crop growth process, either by promoting or reducing growth. Besides the well-established functions, which modify a maximum growth rate r_{max} given available water or nutrients, this maximum growth rate r_{max} can be adapted based on multitrophic interactions (Figure IC).

(iv) acknowledge a diversity of regionspecific approaches [20].

Total factor productivity (TFP): has been considered a metric for agricultural sustainability [41,42]. Growth in TFP denotes growth in an index of all outputs subtracted by the growth in an index of all inputs, influenced by changes in knowledge and management [40]. To account for inputs and outputs, such as climate, soils, and biodiversity, for which no markets exist, green TFP, also termed total resource productivity (TRP), has been suggested [46].

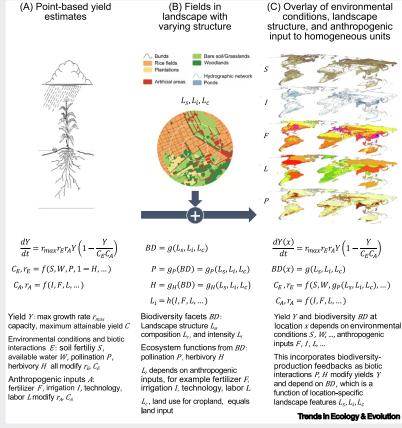


Figure I. Recipe for Embedding Landscape-Scale Biodiversity-Driven Ecological Functions (Multitrophic Interactions) in Global Agroeconomic Models.

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framework to implement BPM, these scaling parameters must additionally consider landscape structure and composition as well as negative externalities due to input intensity, which ensures the interdependence between biodiversity and yields in the yield estimates. This allows a nuanced quantitative assessment of the effects of changes in landscape parameters or input intensity on crop yields and biodiversity. Established model systems, like LPJml [49], InVEST (http://naturalcapitalproject.stanford.edu/software/invest), or SWAT (http://swat.tamu.edu), could serve as testbeds for implementing our analytical framework.

Worked Examples for Pollination

It is estimated that in 23% of cultivated terrestrial landscapes yields are declining, most likely due to land degradation, lack of ecosystem functionality, and declining biodiversity [9]. The association of yield losses with lack of farmland biodiversity-based ecosystem functions is challenging because: (i) the use of chemicals or technical processes may compensate for the loss of ecosystem functions; (ii) the remaining biodiversity may provide the same ecosystem functions; and/or (iii) the negative effects of intensified cultivation methods on biodiversity and yields via BPM may occur with a long time lag [50]. A comprehensive quantitative understanding of the mutualism between biodiversity and production is urgently needed for both global and regional assessments. With few exceptions, such as pollination [51], most ecosystem functions are still poorly understood. Box 2 uses pollination as an example to illustrate how the BPM concept could be implemented for other ecosystem functions.

Knowledge Gaps for Multitrophic Interactions

Data that could contribute to a better process-based understanding of ecosystem functions, quantify the BPM concept, and support implementing the analytical framework are currently being developed through data syntheses that consider landscapes, biodiversity, and agricultural management. Even though these data syntheses are garnering attention [15,52,53], agronomic indicators (management, yields) are often ignored in ecological studies; and biodiversity indicators are underrepresented in agronomic studies [7,25,53,54]. The most crucial knowledge gap, however, arises because ecosystem services, such as biocontrol, are complex and hence difficult to implement in larger models. Biocontrol is a crucial service relevant to all agricultural commodities, including staples that do not depend on animal pollinators [55]; and it applies to the control of both weeds and arthropod pests. In order to overcome these shortcomings, studies that demonstrate trait matching between pests and their natural enemies, that identify how pest densities and damage relate to landscape structure, and that investigate the relative importance of different types of pests for overall yields at global scales (including plant viruses and funguses) are urgently needed.

Properly implemented, models deploying the analytical framework shown in Box 1 will enable researchers to determine the circumstances in which biocontrol provides a more reliable, robust, cost-effective, and ecologically sustainable form of plant protection [56]. While robust models that relate landscape structure to biocontrol are still lacking, there is evidence that a more structured landscape can provide habitat for biocontrol species [15,53,57]. These have the potential to at least partially replace commercial inputs [58] and show a positive relationship between species richness of pollinators and biological control species, while controlling for yield performance [53].

Implications for Global Food Security

A Food and Intensification Gradient Helps to Characterize Countries

A nuanced picture of the BPM in global food production can be derived by characterizing all countries along a food and intensification gradient [27,28]. In regions with high income and



Box 2. Application of Yield Models That Consider the BPM for a Pollination Example

Natural pollination supports production of 75% of all crops [12], and its contribution is estimated at €153 billion worldwide [67]. Pollination is critical for the production of macroand micro-nutrients: 90% of the crops that provide vitamin C, the majority of crops that produce vitamin A, calcium, fluoride, and a large portion of folic acid producing crops are pollinated by animals [68].

Even though a complete global loss of pollination service is unlikely, using it as a thought experiment can help to provide insights into how current agroeconomic models deal with such assumptions [69]. If pollination disappears and all other inputs remain unchanged, then output in the economic model decreases by the percentage loss caused by the loss of pollination [12]. However, the resulting increase in food prices provides an incentive for intensification to mitigate the loss of production [69]. In addition, rising prices on the world market encourage production increases in other parts of the world, particularly where dependence on pollinators is less pronounced.

Given comprehensive information on how crop yields depend on the abundance of pollinating species [12,54,70], we can - in the simplest case - assume a linear relationship between the abundance of pollinating species and the achievable yield (Figure I). If an increase in yield is pursued via intensification, this very likely leads to a reduction in insect species richness and their abundance, which in turn reduces the pollination function [14]. It can be hypothesized that increasing agricultural intensity in landscapes with a high production of pollinator-dependent products will lead to the following pattern (Figure II): (i) yields increase with increasing intensification; (ii) after reaching a threshold (e.g., due to a decrease in pollinator abundance) yields start to decrease; (iii) the maximum level of possible yields is unknown and could also depend on spillover effects (high land-use intensity in the surrounding areas). These negative repercussions of declining biodiversity-based ecosystem function on productivity are not implemented in any global agroeconomic models used for global assessments of food security. In particular, two crucial questions remain unanswered for the pollination case: (i) are potential yields accurate? and (ii) is the nutritional value of agricultural production correctly assessed?

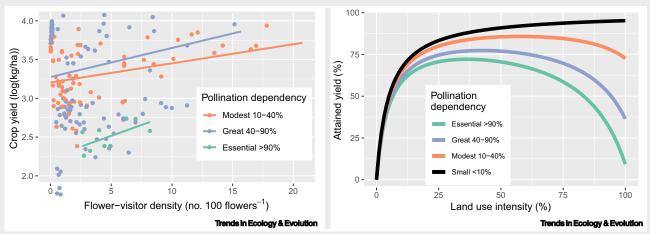


Figure I (left). Yield Increases Differ by Crop Type of Pollinator Dependency Given Different Visitation Rates of Pollinating Species.

Figure II (right). Application of Biodiversity-Production Mutualism Concept. Combining a saturating increase of yields under land-use intensification (black line) with pollination functions, which decline under intensification through increased species loss, provides an application of the BPM concept. This suggests - as a testable hypothesis - a hump-shaped relationship of pollination- dependent yields under intensification (see Figure 1 in main text).

high-input intensity (e.g., Europe and North America), food demand is unlikely to increase because of negligible population growth and advanced or completed dietary transitions. In lowincome countries where input intensity is low [e.g., most of sub-Saharan Africa (SSA)], growth in population and food demand per capita is expected to be rapid. The intermediate cases (e.g., India, Indonesia) exhibit high variations in input intensity, continued population growth at a moderate and declining rate, and ongoing but incomplete dietary transitions. The vast majority of growth in global food demand over the next 30 years is expected to come from these lowincome and middle-income countries.

Implications of the BPM for Low-Intensification Low-Productivity Countries

Our framework suggest that in low-input areas, such as SSA, the scope for increasing production is high, as is the scope for either damaging or preserving biodiversity [10]. In these regions, large parts of the population, especially poor people, depend on agriculture for their livelihoods,



allowing a dynamic agricultural sector to become an effective means of poverty reduction. The BPM concept also highlights that to ensure healthy diets, which eliminate 'hidden hunger' (i.e., the lack of micronutrients in food consumption), functioning ecosystems are needed to provide pollination-based commodities (Box 2). Growth in demand for food is expected to be high, with a likely concomitant growth in food production in these regions.

Consistent with our framework, grain production growth has been rapid in SSA since about 2000, especially when South Africa (high-input-intensity agriculture) and Nigeria (oil exports have slowed agricultural growth) are excluded (Figure 2). With appropriate understanding (i.e., fully considering the BPM concept), a functioning ecosystem can be a partner in the drive to improve livelihoods, reduce malnutrition, and preserve the global environment. Without this understanding, area expansion and intensification in SSA present clear threats to biodiversity. The framework suggests that accounting for BPM while seeking production increases may lead to a more favorable outcome from all perspectives.

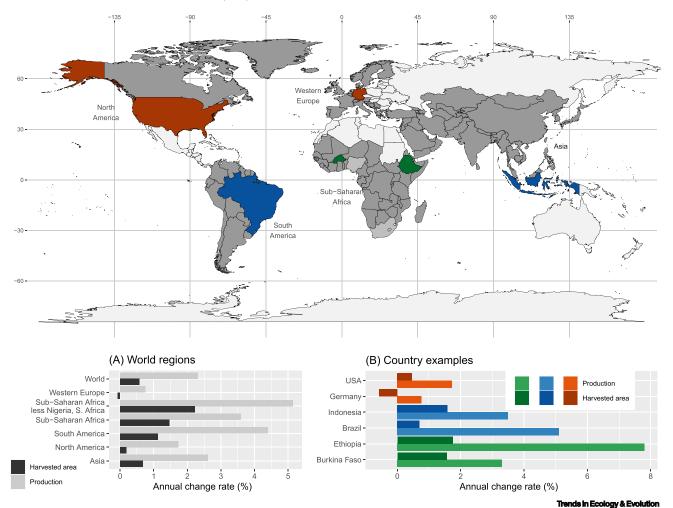


Figure 2. Growth Rates of Cereals Production. (A) shows annualized growth rates of harvested area (dark) and production (light gray) from 2002 to 2005 and 2012 to 2015 for different world regions shaded in gray and labeled on the map. (B) displays the same annualized growth rates for selected countries along the intensification gradient: high-input intensity (red), intermediate cases (blue), and low-input intensity (green). While high-intensity countries have been able to reduce harvested area, all other regions and example countries have increased production through intensification both in terms of land use and yield per hectare. Source: Food and Agriculture Organization of the United Nations - FAOSTAT (www.fao.org/faostat/ accessed August 2018).



The Need for a Paradigm Shift in High-Input Agricultural Regions

In high-input regions, less rapid growth in demand for food creates scope for reducing commercial and natural resource inputs [59]. The BPM framework suggests that this would provide increasing production of positive externalities and reduction of negative ones. Once again, there is evidence that this is happening. In Western Europe and East Asia, the growth of TFP was accompanied by little or no growth in agricultural output and a reduction in the overall amount of conventional inputs, including land, used for agriculture over the last two decades [59]. In the USA, TFP growth has remained strong, while overall input use has remained flat and yield growth has slowed compared with SSA, Asia, or South America [60].

It is important to highlight that a failure to realize adequate food production growth in low-input regions will translate into production pressure in high-input regions via trade linkages. This observation reinforces the need for mechanisms that channel these broadly positive trends in such a way that the production of positive externalities is increased and the production of negative externalities is minimized. In high-input environments, the concept of green TFP can provide a basis for reorienting policies, such as the subsidy system of the EU's common agricultural policy (CAP), towards environmental protection and results-based incentives [61]. In low-input environments, like SSA, green TFP could help research and extension programs clarify the full costs and benefits of alternative agricultural development pathways so that local actors can make informed choices.

Concluding Remarks

The BPM concept provides the basis and a common language for different disciplines, such as agronomy, agroecology, economics, and conservation ecology, to solve a question of utmost importance: How do we manage the terrestrial resources of our planet in such a way that we produce enough healthy food without destroying our life-support system? To respond to this question, it is argued here that a new metric of productivity is required – one that accounts not only for all commercial inputs but also for interactions with the environment. The concept of green TFP, or TRP, is one such measure. Indeed, in 2016 the Group of Twenty (G20) commissioned a white paper on the subject of 'Metrics of Sustainable Agricultural Productivity' [39]. This opinion article features many of the themes raised in the paper, including the importance of extending the traditional TFP measure as well as the need to link farm and landscape impacts in order to capture what is here called BPM.

The BPM concept and its modeling framework (Box 2) links agroecological principles - well known to farmers - with policy-relevant indicators, providing the quantitative base for implementing green TFP and TRP. This can bridge the mismatches between scientific interest in process understanding, farmers' interest in profitability, and decision makers' interest in measurable indicators [33]. Thus, the suggested analytical efforts can support redirection of existing agricultural subsidies towards more economically beneficial and ecologically effective greening measures. We strongly recommend a substantial overhaul of available models and integrated assessment tools. These must account for the inherent feedback between biodiversity, ecosystem function, and resource provisioning, to be capable of identifying possible win-win options in land management that maintain or even increase productivity and halt biodiversity loss (see Outstanding Questions).

Author Contributions

R.S. and T.H. developed the initial idea of the conceptual framework, which was elaborated and finalized by all authors. C.A. focused on implications and perspectives for different world regions, E.A.M. and M.B. on agrobiodiversity and ecological functioning, R.S. on landscape ecology

Outstanding Questions

Along a continuous gradient of land-use intensification, is there is a tipping point after which key facets of biodiversity are unavoidably lost, resulting in diminished and potentially unstable yields? Which aspects of land-use intensification (such as energy, labor inputs, field size, landscape configuration) determine such tipping points? Knowing these major direct drivers supports identifying appropriate measures to stop biodiversity decline in managed landscapes.

How can high-intensity farming systems be managed to support and re-establish biodiversity? Especially landscape-scale measures, which address farmland landscape composition and configuration, are known to enhance farmland biodiversity, but are not considered in agroeconomic models as well as decision making by farmers, who mostly focus on optimally managed fields and largely overlook landscape-scale consequences of their actions.

What is the potential for green TFP to quantify the extent of BPM? Which agricultural policy can be developed in countries with low, intermediate, and high input intensity applying a comprehensive measure, such as green TFP?

What are the specific key facets of land-use intensification for biodiversity in regions of lower land-use intensity (i.e., SSA, India, Eastern Europe)? Are there economic or policy measures available that will reinforce these key elements of the landscape, thereby supporting both biodiversity and agricultural production? Can small-scale farmers be empowered to apply such mechanisms (agroforestry, permaculture, ecological intensification)? How can this development be supported, while avoiding tipping points that lead to biodiversity loss and destruction of ecosystem functioning?

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and modeling, and T.H. on global agroeconomic trade. All authors contributed equally to the development of this opinion article.

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