

APPLIED ECOLOGY

On the functional relationship between biodiversity and economic value

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Biodiversity's contribution to human welfare has become a key argument for maintaining and enhancing biodiversity in managed ecosystems. The functional relationship between biodiversity (b) and economic value (V) is, however, insufficiently understood, despite the premise of a positive-concave bV relationship that dominates scientific and political arenas. Here, we review how individual links between biodiversity, ecosystem functions (F), and services affect resulting bV relationships. Our findings show that bV relationships are more variable, also taking negative-concave/convex or strictly concave and convex forms. This functional form is driven not only by the underlying bF relationship but also by the number and type of ecosystem services and their potential trade-offs considered, the effects of inputs, and the type of utility function used to represent human preferences. Explicitly accounting for these aspects will enhance the substance and coverage of future valuation studies and allow more nuanced conclusions, particularly for managed ecosystems.

INTRODUCTION

The destructive power of humankind on natural ecosystems and the organisms living therein is well documented (1). During the past two decades, awareness that species extinction, habitat loss, and population decline in both natural and managed ecosystems may adversely affect human well-being has increased (2, 3). Economic valuation has emerged as an important tool to illustrate this link between nature and human welfare (3, 4). Increasing public attention has spurred interest in and funding of a number of joint academic and policy initiatives such as the European Biodiversity Strategy to 2020, Aichi targets, Sustainable Development Goals, and the IPBES (Intergovernmental Platform on Biodiversity and Ecosystem Services). These initiatives largely build on the value of ecosystem services concept (Table 1) (3, 5) and the CICES (Common International Classification of Ecosystem Services) cascade (6), in which aspects of biodiversity are valued indirectly as the foundation of ecosystem functioning and service provision (Fig. 1) [see reviews (7–9)].

Evidence from biodiversity–ecosystem function research points toward an increase in ecological benefits with higher levels of biodiversity (10, 11). This relationship has also been hypothesized for the link between biodiversity and economic value. For example, Seddon *et al.* [(12), p. 7] conclude “(...) that by maximizing species, functional and phylogenetic diversity we maximize an ecosystem's value over the long term.” However, empirical studies investigating functional biodiversity (b)–economic value (V) relationships are rare, while the methods and concepts of economic valuation applied are very heterogeneous. This refers, *inter alia*, to the concept of “biodiversity” (discussed in more detail below), ranges of biodiversity levels considered, as well as the type of ecosystem services, their in-

teractions, and the valuation method used. These complexities leave us with an incomplete and unsatisfactory understanding of the functional relationships between biodiversity and economic value.

Despite lacking evidence, the implicit assumption of a positive relationship between biodiversity and economic value prevails in the political arena (4, 13). Gaining an improved understanding of bV relationships and the conditions affecting possible functional forms will be crucial to provide a better scientific footing for future valuation studies, thereby informing future private and public ecosystem management decisions. The objective of this study is therefore to set out a range of possible bV relationships based on theoretical considerations backed up with empirical evidence. Our research is guided by the following question: What are the functional relationships between biodiversity and economic value? We argue that these links may be more complex and more variable than generally assumed. Our focus is on revealing the conditions under which specific functional bV relationships may be expected.

Following the definition by Pascual *et al.* (14), we will refer to “economic value” as the anthropocentric and instrumental values, quantified by direct or indirect use and nonuse values of biodiversity, which we describe in more detail in the following section (see also Table 1). We follow the premise that the economic value of biodiversity may be affected by many intermediate steps, as illustrated in Fig. 1. We build on the three-step effect CICES cascade as a mechanistic model to link economic value to biodiversity. We review how methodological choices may affect the functional relationship of links between biodiversity, ecosystem functions, services, and values and how these may ultimately affect the expected bV relationships.

We start by describing the cascade model, providing a brief review of individual links along the cascade. These sections draw on an extensive body of biodiversity–ecosystem functioning and ecosystem service research. The next section discusses important shapes of possible bV relationships (Fig. 2), which have been derived from stylized mathematical functional relationships informed by theoretical and empirical evidence. These relationships are conceptual in nature and are useful in illustrating how economic value may be influenced by changes in biodiversity. Last, we outline how the conditions identified to affect bV relationships could be incorporated in future valuation studies. With this study, we hope to contribute to an improved

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Table 1. Definitions used in this study (direct quotations from corresponding sources if not denoted otherwise).

| Term | Definition | Source |
|----------------------------------|---|---|
| Biodiversity | The variability among living organisms from all sources, including inter alia terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are part. Biodiversity includes diversity within species, between species and between ecosystems | (5) following the 1993 Convention on Biological Diversity |
| Ecosystem function | The transfer of energy, material, organisms or information among the components in an ecosystem | (25) based on (24) |
| Ecosystem service | The aspects of ecosystems utilized (actively or passively) to produce human well-being | (13) |
| Value | The contribution of an action or object to user-specified goals, objectives or conditions | (5) |
| Utility | A measure of satisfaction or relative preference | (3) |
| Intrinsic value | Inherent value that is the value something has independent of any human experience or evaluation. Such a value is viewed as an inherent property of the entity (e.g. an organism) and not ascribed or generated by external valuing agents (such as human beings) | (14) |
| Instrumental value | The value attributed to something as a means to achieve a particular end such as human well-being | (14) |
| Economic value | Economists group values in terms of “use” or “nonuse” value categories, each of which is associated with a selection of valuation methods. Use values can be both direct and indirect and relate to the current or future (option) uses. Direct use values may be “consumptive” (e.g. drinking water) or “nonconsumptive” (e.g. nature-based recreational activities). Indirect use values capture the ways that people benefit from something without necessarily directly seeking it out (e.g. flood protection). Nonuse values are based on the preference for components of nature’s existence without the valuer using or experiencing it and are of three types: existence value, altruistic value and bequest value | (14) |
| Stated preference | Consumer preferences are understood through questions regarding WTP or willingness to accept | (3) |
| Uncertainty | A broad concept meaning limited knowledge about the future, present, and past. Knight (60) distinguishes between risk (events can be quantified by probabilities) and uncertainty (events cannot be quantified by probabilities). Walker <i>et al.</i> (61) define five levels of uncertainty: (i) clear enough future (with sensitivity information); (ii) alternate futures with probability; (iii) alternate futures can be ranked according to likelihood; (iv) multiplicity of alternate futures, no ranking possible; (v) unknown future. Our examples mainly assume type 2 uncertainty; in Discussion, we also mention studies dealing with type 4 uncertainty | Based on (60, 61) |
| WTP | The maximum income that an individual would be willing to give up to gain something good, such as improvement in environmental quality, or to avoid something bad, such as a decrease in environmental quality | (113) |
| Willingness to accept | The minimum monetary compensation that an individual would be willing to accept to forgo something good, such as improvement in environmental quality, or to put up with something bad, such as a decrease in environmental quality | (113) |
| Revealed preference | A method to assess possible value options or to define utility (consumer preferences) based on the observation of consumer behaviour [estimated for example through the travel cost method, or hedonic pricing e.g. by using real estate prices as a surrogate market for clear air or aesthetic views] | (3) (extended) |
| Production function | A function used to estimate how much [biodiversity and/or] a given ecosystem service (e.g. regulating service) contributes to the delivery of another service or commodity which is traded on an existing market | (5) |
| Externality | A consequence of an action that affects someone other than the agent undertaking that action and for which the agent is neither compensated nor penalized through the markets. Externalities can be positive or negative | (5) |
| Social costs and benefits | Costs and benefits as seen from the perspective of society as a whole. These differ from private costs and benefits in being more inclusive (all costs and benefits borne by some member of society are taken into account) and in being valued at social opportunity cost rather than market prices, where these differ; sometimes termed “economic” costs and benefits | (5) |
| Benefit transfer | Economic valuation approach in which estimates obtained (by whatever method) in one context are used to estimate values in a different context | (5) |
| Insurance value | Decrease of the risk premium due to a (marginal) change in the level of biodiversity. The risk premium is the reward required by a risk-averse person for accepting a higher risk or, in other words, the amount of money that generates the same utility (for a risk-averse decision-maker) between the two situations of receiving for sure the expected return minus the risk premium or facing the risky (random) return | Own definition inspired by (114) |
| Option value | The WTP a certain sum today for the future use of an asset | (115) |

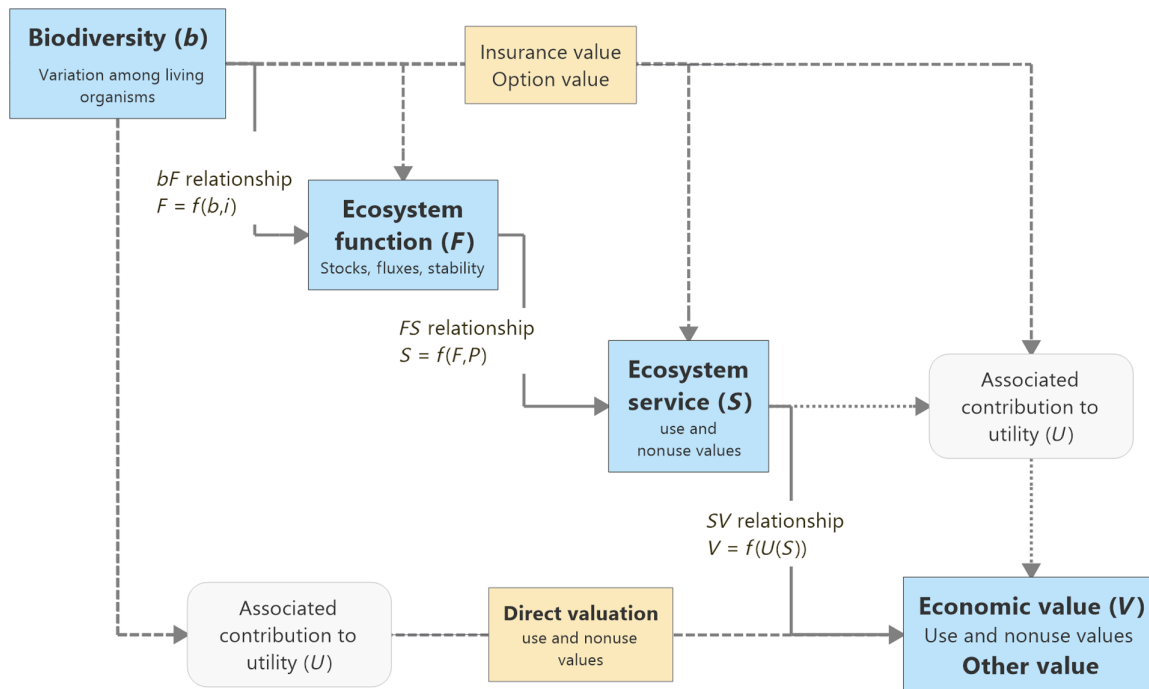


Fig. 1. Underlying cascade and types of values for linking biodiversity with economic value. Taken from Potschin and Haines-Young (6) with small alterations and extensions. Blue boxes follow the indirect valuation pathway (solid lines), and yellow boxes include direct valuation (dashed lines) or combinations of both. For definition of terms, see Table 1. Abbreviations used in blue boxes are also used for mathematical representations in the text, Table 2, and Supplementary Methods.

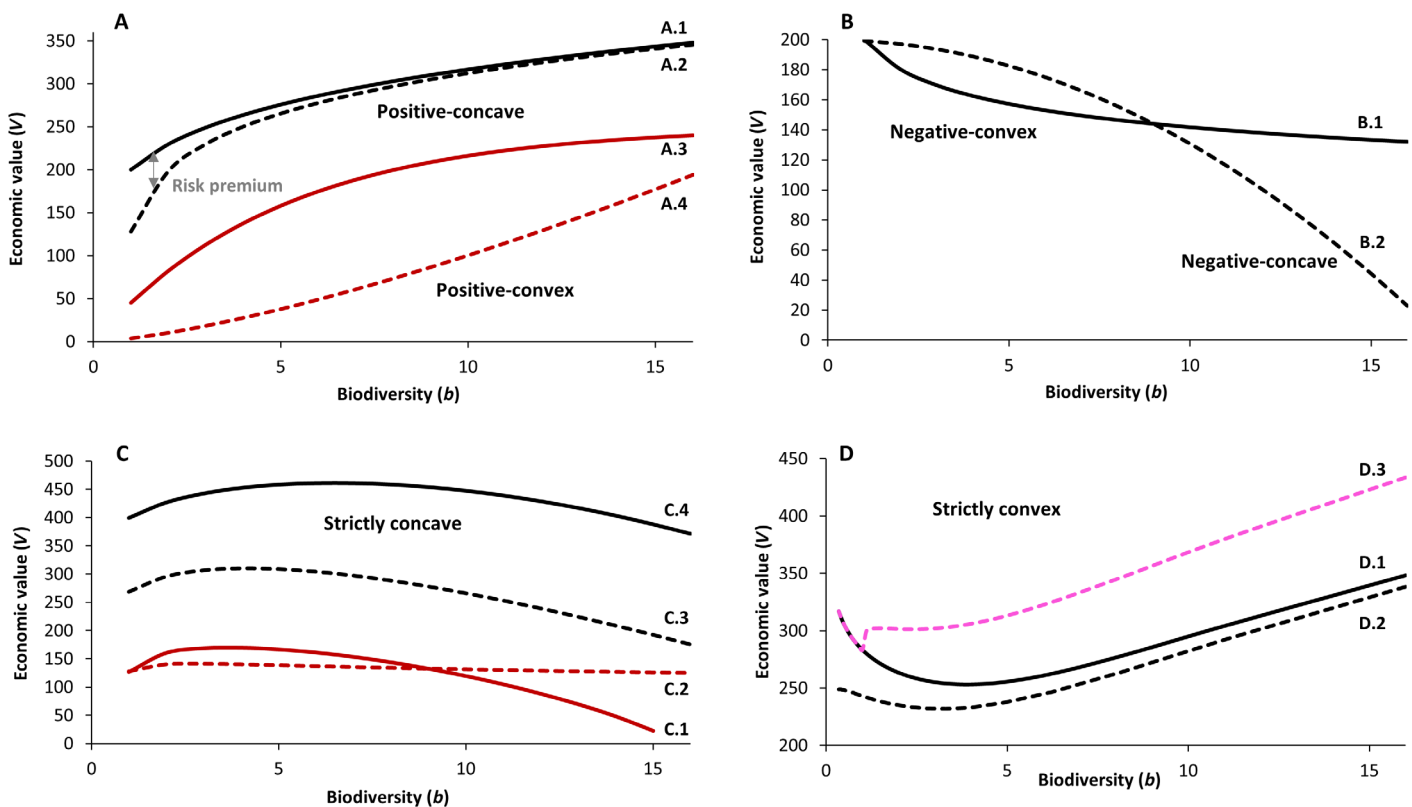


Fig. 2. Plausible biodiversity–economic value (bV) relationships derived from theoretical considerations and empirical examples reviewed here. See Table 2 and Supplementary Methods for detailed description and assumptions of example relationships depicted here. (A to D) Economic value is given in monetary units, and biodiversity is given in number of species (see Supplementary Methods for numerical examples). For A.3, the x axis has to be multiplied by a factor of 100.

understanding of bV relationships, thus informing future development and application of interdisciplinary valuations studies, oriented toward a better means of including biodiversity in private and public decision-making.

A CASCADE LINKING BIODIVERSITY TO ECONOMIC VALUE

The value of biodiversity has been described as the result of a cascade of links from biodiversity (b) through ecosystem functions (F) to ecosystem services (S) to economic value (V) (Fig. 1) (6). Costanza *et al.* (4) argue that a cascade is not suitable for representing complex, non-linear relationships and feedbacks between biodiversity and economic value. However, we are convinced that a cascade model is helpful for investigating how these relationships could be untangled and how they contribute to the shape of the overall bV relationship, especially in cases where there are nonlinearities. We extend the cascade depicted in Fig. 1 according to suggestions by Bartkowski (15) to consider aspects of uncertainty. We first describe the current understanding of these individual links, which will allow us to deduce the resulting shape of the bV relationship, which is our primary focus.

Biodiversity–ecosystem function relationships

The term biodiversity was coined by Wilson (16) as a shortened version of “biological diversity.” At first glance, the concept can be simple: “biodiversity is the sum total of all biotic variation from the level of genes to ecosystems” (Table 1) (17). While these simplified definitions are still frequently used in economic valuation (15), the multi-dimensional nature of biodiversity as understood in ecology requires a range of different metrics to describe its different aspects (17). Modern ecological research considers the number of species (18), abundance-weighted species richness and evenness of species distributions (19), functional diversity (i.e., the diversity in functional attributes or traits in a community) (20), phylogenetic diversity (i.e., the evolutionary relatedness in a community) (21), and genetic and phenotypic diversity among and within species (22). Most commonly used as a measure of biodiversity is the number of species, which we will use for simplicity in the following text and in the empirical examples, when not noted otherwise.

The persistence of ecosystems requires the continuous flow of energy and the recycling of matter (23). The transfer of energy, material, organisms, or information among the components in an ecosystem is called an ecosystem function (Table 1) (24, 25).

Classically, biodiversity research is interested in understanding the abiotic and biotic drivers of the diversity of organisms in an ecosystem. The relatively young field of biodiversity–ecosystem functioning (bF) research emerged around 1990. This field considers biodiversity itself as a driver of ecosystem properties, thus asking questions about the functional importance of biodiversity (26). The past three decades have seen an increased interest in this question (7, 27). Biodiversity experiments that manipulate species richness while excluding confounding effects are an important tool to test causal relationships between biodiversity and ecosystem functions (28). Early and very influential biodiversity experiments were set up in the United States in Cedar Creek, MN (29) by the BIODEPTH consortium in Europe (30) and in the United Kingdom (31). These and subsequent biodiversity experiments [the Jena Experiment described in (32)] have resulted in more than 570 independent manipulations of species richness that now form the foundation of our understanding of the effect of biodiversity on ecosystem functions.

The main conclusion from bF research of the past decades is that a low diversity in an assemblage is associated with a lowered mean level of many ecosystem functions and is often associated with an increase in the coefficient of variation of the level of the functions (11, 33, 34). Several meta-analyses support this conclusion in terrestrial [e.g., (35, 36)] and marine (37) ecosystems.

Species richness and ecosystem function relationships typically are positive-concave curves that frequently saturate at low levels of species richness, e.g., when three to six species are present in the system (30). These saturating relationships have been taken as support for the redundancy hypothesis (38, 39), which proposes that high functioning can be achieved with only a few species. However, redundant species may contribute to maintaining ecosystem functions when other species are lost or under changing environmental conditions (40), referred to as an ecological insurance effect (40, 41). A turnover in the identity of species contributing to a particular function may increase the cumulative number of species sustaining functioning over time (42, 43). Last, when considering multiple functions simultaneously, the number of species contributing to ecosystem multifunctionality is generally higher than the number of species needed for single functions (44, 45).

Biodiversity experiments are deliberately conducted under controlled conditions to investigate the effects of biodiversity independent of other confounding factors. This has sparked a long-standing debate about the questions of whether, and under what conditions, results from these biodiversity experiments can be transferred to the natural world and to managed ecosystems (46, 47). In these natural or managed “real-world” systems, there are many environmental and management factors that are drivers of ecosystem functions in addition to and interacting with biodiversity (48). Consequently, building on bF research, we may thus assume that the ecosystem function F depends on biodiversity (b) and may also depend on human inputs and management (i), such as fertilizer or pesticides.

$$F = f(b, i) \quad (1)$$

Ecosystem functions and ecosystem services

The idea of “ecosystem services” has undergone a process of approaching an appropriate definition (Table 1) [e.g., (3, 5, 13, 49, 50)]. This can now be summarized as contributions to human well-being that people can experience from natural processes, patterns, and structures (i.e., ecosystem functions *sensu lato*). Generally speaking, all definitions cover the different aspects of ecosystems from the perspective of human well-being (51). This implies that an ecosystem function can only be a service if a demand is identified. Ecosystem functions would thus form the capacity of ecosystems to provide services (52). This indicates that all services are related to functions, while, vice versa, ecosystem functions that do not result in a service exist. This strong link between ecosystem functions and services might not be fully applicable for cultural services, which often include human interventions to create a service [e.g., cultural landscapes and recreational values (53)]. Social and behavioral sciences have largely worked independent of the service concept to analyze the importance of nature’s cultural services for people. However, it has also been shown that models can link cultural and aesthetic services with functions [i.e., ecosystem structures and processes from a landscape perspective (54)]. Cultural services may then be integrated into the concept of ecosystem services (55), and indicator sets have been suggested in the context of the national-level mapping [e.g., (56)].

For our present purposes, we assume that consistent and quantifiable links exist between ecosystem functions and services, which

may be used as a basis for valuation. We exemplify these links for a single or bundled ecosystem service(s), S , which is dependent on one or more ecosystem functions (see Eq. 1) and on an indicator P , showing if and how strongly this ecosystem function is in demand.

$$S = f(F, P) \quad (2)$$

P forms a link to valuation. It may be represented by a price or social benefits for one unit of an ecosystem function, as described below.

Valuation of ecosystem services and biodiversity

To provide an analytical framework, we focus on how changes in biodiversity-related ecosystem functions and services affect peoples' utility either directly or indirectly. Utility is a concept for measuring peoples' degree of satisfaction and thereby the subjective value people assign to something in making choices. A utility function is a device that helps us predict how people will make choices between alternatives and gives one way of representing human well-being. A benefit is a specific advantage being valued or its contribution to overall utility, for example, the opportunity for outdoor recreation. We refer to economic valuation as an attempt to measure human preferences for a good. Theoretically, economic value is the total area under the demand curve for a good or service (see fig. S1A), but this information is not usually available for many aspects of biodiversity and the services it supports.

In Fig. 1, we differentiate between two ways of estimating the contribution of biodiversity to economic value, referred to as direct and indirect. First, people may obtain direct benefits from the presence, diversity, and abundance of organisms or ecosystems. For example, people can experience greater utility from walking in woodlands with more bird species than fewer species and may be happier knowing that a new marine protection area is conserving cold water corals, even if they themselves cannot visit the corals. These aspects generate a mix of use and nonuse values, the latter often being distinguished into existence, bequest, or altruistic values [see Table 1 and (57)]. These values directly affect peoples' utility to varying degrees, in which interperson variability is referred to as preference heterogeneity.

Building further on the cascade approach, we can also quantify the benefits of biodiversity in an indirect way. For instance, when higher species diversity results in an increased net primary production (NPP) and therefore enhances provisioning and/or regulating services or when biodiversity provides pest control affecting marketable food products or if high overall forest plant diversity is needed to obtain specific pharmaceutically valuable species, then peoples' utility is indirectly increased by these effects (see solid lines and blue boxes in Fig. 1). This type of valuation builds on all steps along the cascade using ecosystem services as an intermediate link between the ecological and economic context. Ecosystem services can be characterized as market-based private goods (e.g., timber outputs), as nonmarket-based quasi-public goods (e.g., the opportunity for recreation in forests), and as positive externalities (e.g., carbon sequestered by means of forestry) (Table 1). For many of the biodiversity-dependent goods, markets do not exist, meaning that market prices cannot be used to measure the value of increases in their supply.

For both types of valuation—the direct and indirect bV approaches (both dashed and solid lines in Fig. 1)—the valuation of nonmarket goods may build on among other things: (i) the avoided (social) costs when using ecosystem structures and processes rather than alternatives, (ii) the changes in the service's market value caused by a nonmarket

service serving as productive inputs (e.g., the effects of pollination on crop outputs) (58), or (iii) peoples' willingness to pay (WTP) for changes in the level of biodiversity or for an affected service. WTP attempts to quantify the expected utility experienced by a person from consuming a certain good or receiving a specific service (59).

As Bartkowski (15) shows, estimating “uncertain-world values” (depicted in the upper yellow box and upper dashed lines in Fig. 1) is another important aspect where biodiversity is indirectly linked to notions of economic value. Here, we consider two facets of uncertainty connected to economic value. Uncertainty relates first to the fluctuation of services provided by a system around an estimated mean. Second, uncertainty may also be associated with potential discovery of additional species and their so far disregarded values, creating a WTP for options associated with biodiversity-rich ecosystems. Both concepts require that fluctuations or probabilities may be measurable and appropriately assigned. Such a situation is often referred to as describing “risk” (60) or as level 2 uncertainty, where alternate futures with identifiable probabilities exist (Table 1) (61). However, these estimations, for example, of standard deviations of provided functions or probabilities of discovery also involve high uncertainty. Therefore, we here use risk and Knightian uncertainty interchangeably following Bikhchandani *et al.* (62), assuming that some quantification of uncertainty is needed to understand its economic consequences.

One way of economically integrating these uncertain-world values is by a concave utility function characterized by diminishing marginal utility. On the basis of this utility curve, an insurance value may arise if economic return fluctuations are reduced by growing a higher variety of crop species, whose return fluctuations are independent or negatively correlated. A reduction in return fluctuations, excluding any effects of crop diversity on the expected (average) return, will increase utility for risk-averse persons, while he or she will require a reward (a “risk premium”) for accepting higher levels of risk (Table 1) (62). Therefore, a risk-averse farmer would benefit from using a higher agrobiodiversity of crop species as a production input as well as a risk hedging strategy (63). Building on the simple proverb of “don't put all your eggs in one basket,” the farmer would require a smaller risk premium when using higher agrobiodiversity for production. Baumgärtner (64) and Finger and Buchmann (65) estimated an insurance value of biodiversity as the decrease of the risk premium when biodiversity increases by one unit.

Concerning our second example of uncertainty, biodiversity may also offer option values (Table 1) (15). Higher levels of biodiversity may, for instance, provide future but currently unknown commercial opportunities in an uncertain world, such as the potential use of specific species for pharmaceutical products or using biodiversity as a library on genetic information for future screening (66). A large fraction of prescription drugs are derived from natural products, while genetic information is also important for plant breeding. Bioprospecting attempts to realize this potential (67). Consequently, biodiversity generates an option value concerning currently unknown future benefits (15). In addition, the economic theory of real options brings an aspect of flexibility into consideration (68). For example, one can postpone decisions on invasive species control to obtain better information to improve policy responses (69). In natural resource management, the value of these options depends on the degree of flexibility they provide for decision-makers (70), where flexibility is better facilitated by resistant compared to vulnerable ecosystems (71). Empirical evidence also suggests that (economic) resistance to shocks may depend on the level of biodiversity in some situations (72).

RESULTING SHAPES OF BIODIVERSITY–ECONOMIC VALUE RELATIONSHIPS

On the basis of this economic background of valuation, we postulate that the main contribution of biodiversity to economic value (V) is associated with facilitating and supporting ecosystem services. Utility (U) is thus created indirectly as $U(S)$ (Fig. 1, solid lines). The contribution of biodiversity is also a direct one, i.e., $U(b)$, when people obtain benefits from the presence, diversity, and abundance of organisms or ecosystems (lower dashed line in Fig. 1). Summarizing both types of valuation, economic value may then be described as

$$V = f(U(S, b)) \quad (3)$$

Given the cascade, $F = f(b, i) \rightarrow S = f(F, P) \rightarrow V = f(U(S))$ (Fig. 1), we will focus mainly on the indirect contribution of biodiversity to economic value, as this contribution may be established using the well-researched biodiversity–ecosystem function relationships. We derive four hypothetical bV relationships illustrated in Fig. 2. The relationships include positive-concave and positive-convex (Fig. 2A), negative-concave and negative-convex (Fig. 2B), and strictly concave (Fig. 2C) and (quasi-) or strictly convex (Fig. 2D) functional forms. We suggest that the functional relationships are driven by five main conditions: (i) the type of bF relationship, (ii) the number and type of ecosystem services considered, (iii) the trade-offs between services or between risk and return, (iv) whether effects of “synthetic” inputs are considered, and (v) the type of utility function used to represent human preferences.

For each functional form, we discuss the conditions under which it may be expected and how a potential mathematical formulation may look (Table 2). The rationale for each mathematical representation and the underlying assumptions are described in more detail in Supplementary Methods. We will then discuss how well these relationships are supported by empirical evidence. Our starting point will be the most frequently assumed positive bV relationship.

Positive-concave or positive-convex relationships

A positive-concave relationship between biodiversity and economic values (Fig. 2A) means that economic value increases with additional species in the ecosystem at a diminishing rate. The response in economic value per additional unit of biodiversity is large when starting at a low level of biodiversity and decreases for higher levels (Fig. 2A, A.1). This relationship may result from a positive-concave bF relationship, frequently observed for single ecosystem functions, such as NPP (73–75). O’Connor *et al.* (76) have, for example, described the relationship between a change in species richness on biomass (here F) (Table 2) as a power function

$$F(b) = \alpha b^\beta \quad (4)$$

with α and β being coefficients, defined as $\alpha > 0$ and $0 < \beta < 1$ for a positive-concave bF relationship. Provided that a demand for the ecosystem function exists and that the economic value is proportional to the ecosystem service, a positive-concave bV relationship results. This proportional relationship builds on two main assumptions: First, the price P (Eq. 2) attributed to each species is identical for all species, which means that the ecosystem service provided (denoted as S in Eq. 2) is considered a homogeneous good (Table 2, column “Type of S good”). This condition would, for example, apply to carbon

sequestration where there are no differences in the value of a ton of carbon sequestered by different species [e.g., (74)]. The commercial market price for hay might, however, differ between grassland species because of differences in quality and consumer preferences (Table 2) [e.g., (77)]. Second, the linear relationship between S and V (Eqs. 2 and 3) provides that the relative increase in satisfaction gained from receiving an additional unit of S is constant for all levels of S . This could be represented by a linear utility function $U(S)$ (Eq. 3). Such a utility function assumes that decisions are taken independently from risks (i.e., assuming risk neutrality) and wealth of the decision-makers (see Table 2, column “Human preferences”).

A recent example for a positive-concave bV relationship is a study by Liang *et al.* (75) (Fig. 3A). On the basis of a positive-concave relationship between biodiversity and NPP derived from experimental plots, Liang *et al.* (75) suggest a high commercial wood value associated with the biodiversity of species-rich forests. The underlying assumption is that the economic value added from forests is directly affected by, and proportional to, forest productivity (i.e., biomass production; see green triangles in Fig. 3A). Here, biomass is directly related to a mean commercial value, meaning that wood is considered a homogeneous good, for which quality and species identity are not explicitly considered.

Similarly, Hungate *et al.* (74) found a positive-concave bV based on the social costs of carbon (Table 1) estimated for an increasing number of species in pasture systems (see magenta circles in Fig. 3A). While these studies focus on a single ecosystem service—wood production and carbon storage—Costanza *et al.* (73) used an aggregated value, where ecoregion-specific NPP values were coupled with a benefit transfer function based on an earlier study by Costanza *et al.* (78) (yellow circles in Fig. 3A). Using this type of aggregation, trade-offs between services are assumed to be absent (see Table 2, column “Trade-offs/social costs or benefits”), and quite different individual preferences are aggregated to derive economic values (79).

The studies mentioned above applied linear utility functions, and this rather strong assumption has been relaxed by Finger and Buchmann (65) using a positive-concave utility function to assess average returns from grassland yields and their variance (blue diamonds in Fig. 3A). This utility function accounts for the effects of uncertainty in ecosystem service provision on peoples’ preferences. Under the presence of uncertainty, the notion of “expected utility,” $E[U(S)]$, is used. Given a concave utility function, the expected utility of the same average economic return then increases with decreasing variance. Finger and Buchmann’s study assumed a positive-concave bF relationship for grassland biomass yield and a negative-convex bF relationship for the variance of yield, which is in line with findings from biodiversity experiments (11). This constitutes two positive effects (a double dividend) of increasing biodiversity, here quantified by Shannon diversity index, namely, increased mean provision and reduced variability of the studied service. Combining a concave utility function with a concave bF reinforces the positive-concave bV relationship rather than altering the general relation (Table 2 and Fig. 2A, A.2).

Concave, positive relationships have also been found for the economic value of additional species in the pharmaceutical industry (80). As the functional relationship published by Simpson *et al.* (80) shows (Fig. 3B), stochastic considerations—known as sampling effects in bF research—may constitute a positive impact of biodiversity on economic value (Fig. 2A, red solid line, and Table 2, A.3). When species richness increases, the probability of finding a new species of value for the pharmaceutical industry rises.

Table 2. Description of conditions (columns) for hypothesized biodiversity (b)–economic value (V) relationships (lines) as depicted in Fig. 2. Numbers in the first column refer to denomination of functional relationships in Fig. 2 (bF, biodiversity-function relationship; S, ecosystem service). For further explanation and derivation of mathematical functions, see the Supplementary Materials. In our example mathematical representations, we refer to biodiversity as the number of species (see the Supplementary Materials for numerical examples).

| Number | bV relationship | bF relationship | Effects driving bF | Agrochemical inputs | Type of S good | Trade-offs/ social costs or benefits | Human preferences | Possible mathematical representation* |
|--------|----------------------------------|-------------------------------------|---|------------------------|------------------------|--------------------------------------|-------------------------------|---|
| | Relationship of cascade affected | bF | bF | bF-FS | SV | SV | SV | |
| A.1 | Positive-concave | Positive-concave | Biological synergies† | No | Homogeneous | No | Linear utility | $V(b) = PF(b)$ $F(b) = \alpha b^\beta \quad 0 < \beta < 1$ |
| A.2 | Positive-concave | Positive-concave | Biological synergies/ stochastic (averaging effect) | No | Homogeneous | No | Concave utility (risk averse) | $V(b) = \overline{PF(b)} - 0.5 \frac{\gamma}{PF(b)} \text{var}(PF(b))$ $\overline{F(b)} = E[\alpha b^\beta]; F(b) = \alpha b^\beta$ $0 < \beta < 1, \gamma > 0$ |
| A.3 | Positive-concave | Positive-concave | Stochastic (sampling) effect | No | Assumed as homogeneous | No | Linear utility | $V(b) = PF(b)$ $F(b) = 1 - (1 - p)^b$ $P > 0$ |
| A.4 | Positive-convex | Positive-convex | Biological synergies | No | Homogeneous | No | Linear utility | $V(b) = PF(b)$ $F(b) = \alpha b^\beta \beta > 1$ |
| B.1 | Negative-convex | Negative-convex | Biological synergies | No | Homogeneous | No | Linear utility | $V(b) = PF(b)$ $F(b) = \alpha b^\beta \beta < 1$ |
| B.2 | Negative-concave | Negative-concave | No synergies | No | Homogeneous | No | Linear utility | $V(b) = PF(b)$ $F(b) = \alpha(1 - (b_m + 1)^{-\beta} b^\beta)$ |
| C.1 | Strictly concave | Negative-concave | Stochastic (averaging) effect | No | Homogeneous | Risk return | Concave utility (risk averse) | $V(b) = \overline{PF(b)} - 0.5 \frac{\gamma}{PF(b)} \text{var}(PF(b))$ $\overline{F(b)} = E[\alpha(1 - (b_m + 1)^{-\beta} b^\beta)]$ $F(b) = \alpha(1 - (b_m + 1)^{-\beta} b^\beta)$ $\beta > 1, \gamma > 0$ |
| C.2 | Strictly concave | Negative-convex | Biological synergies/ stochastic (averaging) effect | No | Homogeneous | Risk return | Concave utility (risk averse) | $V(b) = \overline{PF(b)} - 0.5 \frac{\gamma}{PF(b)} \text{var}(PF(b))$ $\overline{F(b)} = E[\alpha b^\beta]; F(b) = \alpha b^\beta$ $\beta < 0, \gamma > 0$ |
| C.3 | Strictly concave | Positive-concave | Biological synergies | No | Heterogeneous | Various prices | Linear utility | $V(b) = \overline{P(b)} F(b)$ $F(b) = \alpha b^\beta$ $0 < \beta < 1$ |
| C.4 | Strictly concave | Positive-concave + negative-concave | Biological synergies | No | Homogeneous | Two S | Linear utility | $V(b) = P_1 F_1(b) + P_2 F_2(b)$ $F_1(b) = \alpha_1 b^{\beta_1}$ $F_2(b) = \alpha_2(1 - (b_m + 1)^{-\beta_2} b^{\beta_2})$ $0 < \beta_1 < 1, \beta_2 > 1$ |
| D.1 | Strictly convex | Positive-concave | Biological synergies | Fertilizer/ pesticides | Homogeneous | No | Linear utility | $V(b, i) = PF(b, i)$ $F(b, i) = \alpha \left(\frac{b}{b_m} b + \left(1 - \frac{b}{b_m} \right) \omega i \right)^\beta$ $b = b_{\max} i^{-\theta}$ |

continued on next page

| Number | <i>bV</i> relationship | <i>bF</i> relationship | Effects driving <i>bF</i> | Agrochemical inputs | Type of <i>S</i> good | Trade-offs/ social costs or benefits | Human preferences | Possible mathematical representation* |
|--------|------------------------|------------------------|---------------------------|------------------------|-----------------------|--------------------------------------|-------------------|--|
| D.2 | Strictly convex | Positive-concave | Biological synergies | Fertilizer/ pesticides | Homogeneous | Social costs | Linear utility | $V(b, i) = PF(b, i) - iC$ $F(b, i) = \alpha \left(\frac{b}{b_m} b + \left(1 - \frac{b}{b_m} \right) \omega i \right)^\beta$ $b = b_{\max} i^{-\vartheta}$ |
| D.3 | Strictly convex | Positive-concave | Biological synergies | Fertilizer/ pesticides | Homogeneous | Social benefits | Linear utility | $V(b, i) = P_1 F_1(b, i) + P_2 F_2(b)$ $F_1(b, i) = \alpha_1 \left(\frac{b}{b_m} b + \left(1 - \frac{b}{b_m} \right) \omega i \right)^{\beta_1}$ $F_2(b) = \alpha_2 (b - 1)^{\beta_2}$ $b = b_{\max} i^{-\vartheta}$ |

* $V(b)$ is the economic value depending on biodiversity, b . b is the number of species in our examples. b_m is the maximum biodiversity. $F(b)$ is the ecosystem function, depending on b . P is an indicator for demand; in our examples, it is a price or a (saved) social cost. $P(b)$ is an average price, depending on biodiversity, b . $E[\cdot]$ is an expected value; α , β , γ , ω , and ϑ are coefficients. $\gamma > 0$ quantifies the constant relative risk aversion. P quantifies the probability for a commercial success when testing a species for pharmaceutical use. i is a human input. $\text{var}(\cdot)$ is the variance. †With biological synergies, we refer to the observation that two or more organisms may produce a greater result than each would achieve individually. This may be due to ecological facilitation, which benefits at least one species in terms of increased productivity, reduced physical stress or disturbance (particularly in forest ecosystems), or reduced predation. We distinguish these effects from stochastic averaging and sampling effects described in more detail in the text.

As a third form of a positive *bV* link, we conceptualize a positive-convex relationship (Fig. 2A, A.4). For this case, the increase in economic value per additional biodiversity unit would be increasingly larger at a higher biodiversity level. Such a relationship could arise from positive-convex *bF* relationships, as hypothesized by Mora *et al.* (81), for which empirical evidence is so far lacking. Given a homogeneous good and a linear utility function, a positive-convex *bF* link would translate into a positive-convex *bV* (Table 2, A.4).

In conclusion, the evidence collected above suggests a positive-concave *bV* relationship under certain conditions. These include the valuation of a single ecosystem service of interest or the absence of trade-offs between multiple ecosystem services or risks and returns, strong ecological synergies and/or sampling effects, and the consideration of a homogeneous ecosystem output—such as carbon sequestration—for which species identity and quality are less relevant. It mostly requires a linear utility function or a concave utility function when variability of the level of *F* is considered.

Negative-concave or negative-convex relationships

A positive *bF* link was a precondition for the results presented above. However, ecosystem functions are not always positively linked with species diversity, possibly resulting in a negative, either concave or convex *bV* relationship (Fig. 2B). For instance, Costanza *et al.* (73) showed in an empirical study of various ecoregions of North America that the NPP of low-temperature regions—as opposed to high-temperature regions—was negatively correlated with species richness. Combining NPP with an economic value function that considers multiple services created a negative *bV* relationship for these low-temperature regions. In agreement with this finding, a recent study by Sandau *et al.* (46) found negative *bF* relationships for specific conditions in a grassland experiment, where colonization from the surrounding species pool was allowed. Hence, a negative *bF* may turn a positive-concave or positive-convex relationship into a negative one, even when assuming a homogeneous service good, a linear utility function, and the absence of trade-offs (Table 2, B.1).

In addition to these rather scarce empirical examples for a negative *bF*, we may theoretically expect these relationships in the absence of biological synergies. This means that we would exclude any beneficial

interactions between species, which are the mechanistic basis for a positive *bF* relationship. This could, for example, be the case when growing crops on separate parcels of a field, thus avoiding the higher complexity of mixed, e.g., intercropping, systems. Growing various parcels of different crops, including those with lower NPP, will inherently lead to a lower average value for this ecosystem function as compared to a monoculture of the most productive species. In the absence of biological synergy and risk aversion, this would lead to a negative *bV* relationship (Table 2, B.2).

Strictly concave relationships

Strictly concave biodiversity–economic value relationships (Fig. 2C) may be found if assumptions deviate from those, described for positive-concave *bV* relationships in terms of (i) a utility function accounting for risk aversion (Table 2, relationships C.1 and C.2), (ii) heterogeneous ecosystem service goods (C.3), or (iii) if trade-offs among multiple services exist (C.4).

As described in the earlier section, risk-averse persons may benefit from a statistical averaging effect associated with biodiversity, which decreases the variability of services and thus enhances expected utility. The portfolio effect is among the main causes for a positive influence of species diversity on the stability of economic returns (65), leading to a positive-concave relationship for risk-averse decision-makers (see Table 2, A.2). However, this provides that there is a double dividend effect, namely, a reduction of risk plus a positive effect of biodiversity on the expected return, for example, through increased yields. If the positive effect of biodiversity on expected return is excluded, accounting for the resulting trade-offs between (economic) risk and expected (average) return, the relationship may turn from a positive-concave to a strictly concave *bV* relationship. This can be exemplified by a stylized farm growing crops on separated parcels (as described above). Therefore, species interactions among crops are largely excluded while allowing efficient agricultural management. Adding additional species to such a land-use portfolio will lead to a strong initial decrease in the standard deviation of economic returns, provided that the return of the different crops is not perfectly correlated [see example in fig. S2 (pink symbols)]. With higher numbers of admixed crop species, this decrease in standard deviation of returns becomes smaller. However, the expected (average)

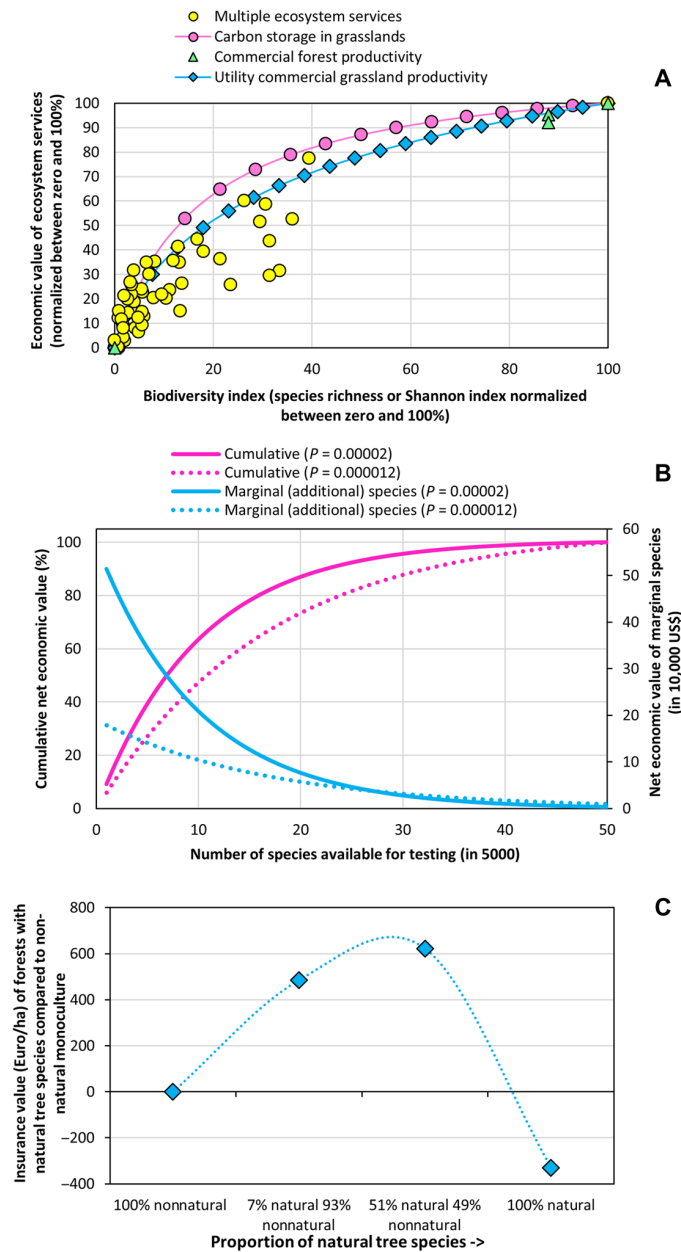


Fig. 3. Empiric examples for bV relationships. (A) Services related to biomass production or carbon sequestration are considered. All values have been normalized between zero (minimum economic value/species richness) and 100% (maximum economic value/species richness). Yellow: Costanza *et al.* (73) estimate a biodiversity (reflected by the number of vascular plants) NPP relationship for certain ecoregions in the United States and couple this function with a function to estimate aggregated economic value published earlier (78). Magenta: Annual economic value of carbon sequestration in grasslands (74) based on a medium scenario for social costs of carbon, when progressively adding grass species to a grassland monoculture [data were adopted from Hungate *et al.* (74)]. The authors report net present values of differences in ecosystem carbon content with an increasing number of grass species over a 50-year period (marginal values) based on social costs of carbon (112) discounted with a constant 4% discount rate. Green: Commercial forest value when species richness (per plot) varies (75). An assumed reduction by one tree species forms high and low economic values close to 100%, while a reduction to only one tree species forms the minimum (zero achievement level). Blue: Utility of commercial value of biomass yields in grasslands depending on Shannon diversity index (65). (B) Marginal and cumulative values of species for pharmaceutical bioprospecting [data are from Simpson *et al.* (80)]. A probability for a commercial discovery, P , of 0.000012 or 0.000020 for each single species and other coefficients according to Simpson *et al.* (80) was assumed to compute upper bounds for marginal species net economic value according to equation 10 of Simpson *et al.* (80). The number n of species available for pharmaceutical testing was varied from 5000 to 250,000. The mathematical products of the respective marginal net economic value and the number of additional species were summed to express the functional relationship between the number of species and the cumulative net economic value in percent. (C) Insurance value of admixing natural tree species into nonnatural forests based on data taken from (85). With nonnatural forest, we refer to a forest plantation made up by a single nonnative tree species. Admixing these stands, poor in species diversity and forest structure, with native tree species [e.g., those suggested by the concept of potential natural vegetation; see, e.g., (83)] would increase naturalness. The insurance value is quantified as the decrease in risk premium (Table 1; see eqs. S7 to S13). Here, we assigned logarithmic utility to each uncertain economic return, which was subsequently averaged. If the economic risk is high (i.e., we have volatile economic return), a high risk premium and a high expected economic return are required. For example, the high risk premium required for a nonnatural forest (Norway spruce) is reduced by about €450 per hectare by integrating 7% natural tree species (European beech) [data: (85); valuation approach: (65)].

return also decreases when adding crops with lower expected return. Capturing these risk/return trade-offs in a concave utility function, as typically assumed for risk-averse people, results in a strictly concave biodiversity/economic utility relationship as surrogate for a bV relationship (fig. S2, orange line, and Table 2, C.1) (82).

In addition to the purely stochastic effect described above, higher levels of naturalness, associated with enhanced native biodiversity, may have a stabilizing effect, also referred to as “insurance value” (see Tables 1 and 2 and Fig. 3C). For example, consider a forest plantation that is planted with either a species maximizing for productivity and profitability (e.g., spruce in Central Europe) or the natural dominant species (referred to as “natural”) of the region (e.g., beech) or a mixture of both (Fig. 3C). Assume a higher survival probability for the non-natural tree species in a mixed, seminatural forest, where a natural species completes the composition. This constitutes a biological synergy, which affects the stability of the economic return (72). Further assume that aspects of biodiversity are represented by an indicator of naturalness of forest structure (83). The proportion of the native tree species can be considered as an indicator for naturalness following Bončina *et al.* (84). Figure 3C shows that the monetarized insurance value (see Table 1 and the Supplementary Materials for more details) is higher for a more diverse, seminatural forest, where the native tree species stabilizes the nonnatural species, compared to a profitable, yet risky, monoculture of the nonnatural tree species. This increase in the insurance value constitutes a positive bV relationship *sensu* Finger and Buchmann (65) (Table 2, A.2). However, in our example, for high proportions (more than 50%) of the natural dominant tree species, the return declines so steeply that the balance between economic return and risk becomes unfavorable. In the dataset used for this example (85), the return variability in beech-dominated stands becomes high, compared to the low average economic return. Consequently, the trade-off between economic return and risk turns the positive-concave into a strictly concave bV relationship (Table 2, C.1). Consideration of risk reduction when using multiple species may even turn a negative-convex bF into a strictly concave bV (as for B.1, see Table 2, C.2).

Our second condition for strictly concave relationships is the consideration of heterogeneous goods (C.3), i.e., differences in the (commercial) quality of ecosystem functions and resulting services produced by specific species or ecosystems. As Binder *et al.* (77) outlined, species richness alone is, from a private producer perspective, less relevant than the identity and relative abundance of species. A farmer would only select those communities that offer the highest utility for each level of species richness. In line with risk/return analysis, this could be considered a species/value efficiency frontier. Binder *et al.* (77) calculated optimal species identity and relative abundance of managed grassland for maximizing the economic (land) value—based on the risk-adjusted (certainty equivalent) present value of the future stream of profits—for each level of species richness. The economic analysis accounted for effects of species composition and interactions on hay quality, quantity, and variability, as well as differences in seed costs. It was found that while the average of compositions showed a positive-concave bV relationship, the economically optimized grassland communities yielded a strictly concave relationship. The same functional relationship was even found for a risk-neutral decision-maker (i.e., with a linear utility function). This important finding demonstrates that bV relationships strongly depend on the species identity and composition of the studied communities, particularly when taking a private producer perspective (Table 2, C.3).

Last, a third case for a strictly concave bV relationship is multifunctionality, which has been defined as the ability to integrate human production with the retention of service flows (86). This means that we focus on multiple services, which build on single or multiple functions and are subsequently valued together or separately. Biodiversity is not always positively linked with all services and their economic values because of trade-offs between functions and/or services (Table 2, C.4) (45). A further complication is that multifunctionality (in terms of functions and services) itself is not a constant but changes depending on the number and identity of considered functions (45, 87). In line with this finding, the economic value attributed to multifunctionality may be expected to change, depending on the type and number of functions/services considered. As an example, with relationship C.4 (Fig. 2C and Table 2), we consider two services. First, we provide a negative bF relationship, characterized by an increasing rate of reduction in the level of F with increasing b (Table 2, C.4). The scenario could occur, for instance, if a farm grows various crops on separated parcels in a compartmental land-use system (88). Second, we assume a concave saturating bF relationship. Within a compartmental land-use concept, such a bF may apply when high compositional crop diversity reduces soil erosion. With increasing numbers of agricultural crops, the harvesting times would become more and more diversified, meaning that the area exposed for erosion would be approximately proportional to $\frac{1}{b}$, where—in an ideal case— b refers to the number of crops. The avoided soil erosion constitutes an economic value, and aggregating both effects results in a strictly concave bV .

In our review, we found very few examples, which account for trade-offs between services in valuation studies [see fig. S3 for one example based on Braat and ten Brink (89)]. The actual shape of the bV relationships assuming trade-offs among functions and services will greatly depend on the valuation of individual services, given that single services are valued and subsequently aggregated. Higher values of provisioning services, compared to those used by Costanza *et al.* (73), could have considerably changed their confirmed positive-concave bV relationship (depicted in Fig. 3A) if trade-offs were included. For example, if maximum levels of biodiversity exclude high levels of food production—so food becomes much more valuable under increasing scarcity—the positive-concave bV relationship described by Costanza *et al.* (73) could become strictly concave, with a possible maximum at intermediate levels of biodiversity. This highlights the importance of a careful selection of valuation and aggregation methods and the use of sensitivity analyses to identify potential functional bV relationships.

Strictly convex relationships

A strictly convex relationship (Fig. 2D) can be interpreted as an indication that higher biodiversity may compensate for greater management intensity and vice versa. Weigelt *et al.* (90) demonstrate equal and high productivity in high-diversity/low-input and low-diversity/high-input grassland systems. Their study suggests that management intensity could substitute for diversity when high productivity is the aim. When constraining environmental heterogeneity using inputs such as fertilizer, irrigation, or pesticides, monocultures may produce very high yields (91). Under these homogenized environmental conditions, high biodiversity is not persistent. In contrast, if environmental heterogeneity is high (i.e., without homogenization), no single species will obtain maximum yield, under all conditions, due to differentiation of niches. Increasing biodiversity will then increase yield. Combining both perspectives results in a strictly convex bF , which may be associated with a similar bV relationship if economic

value is proportional to productivity (Fig. 2D, D.1, and Table 2, column “Agrochemical inputs”).

In addition, the use of plant diversity to replace expensive agricultural inputs suggests a higher economic value from more species-rich ecosystems, if diversity is cheaper than agricultural input or if social costs associated with environmental pollution from chemical inputs may be so avoided. These interdependencies do not alter the strictly convex shape of the bV relationship but may change their maxima, as seen in Fig. 2, where, in D.2, high biodiversity (right end) more than compensates the economic value under high agrochemical inputs (left end). Consequences of increasing the level of biodiversity such as these have rarely been investigated in an economic context, although they could be of particular interest for highly managed ecosystems. Excessive fertilizer usage implies social costs resulting from increased air and water pollution (91). Consequently, a substantial part of the economic value of biodiversity (agrobiodiversity) is the avoided cost of nitrogen pollution, for example, reducing the social costs of nitrogen (SCN). Estimates of the SCN are variable but may be high (92). Keeler *et al.* (92) report a discounted value of monetary damages caused by a change in N, which varied between US\$0.001 and US\$10 per kilogram of nitrogen.

These effects of reducing the short-term social costs of land management are important for informing the long-term perspective. Avoided soil degradation will save long-term costs of soil rehabilitation or replacement (93) and may thus change the strictly convex relationship even further in favor of more biodiverse ecosystems. To illustrate the possible effects of both biodiversity and fertilizer on agricultural yield, we analyzed data for organic and conventional farms using either multi- or monocropping systems, with multicropping referring to growing more than one different crop species on the same field during one growing season [table S1; using data obtained from (94)]. In these systems, monocropping may produce higher agricultural yields than multicropping systems, but only under high N inputs (fig. S4). In contrast, the multicropping system delivers relatively high agricultural production levels at a much lower N input. For example, multicropping may achieve an annual level of production of 4.4 tons per hectare with 80 kg less N input than monocropping. If we assume a very high potential SCN of US\$10 per kilogram of nitrogen, saving 80-kg nitrogen by exploiting agrobiodiversity would yield a present value of US\$ 800 per hectare each year. This demonstrates the importance of the idea of ecological replacement (95) in valuing biodiversity, which may lead to a strictly convex functional bV relationship.

Using this example, we can also account for other nonmarket benefits of biodiversity, for example, considering improved carbon storage in more biodiverse ecosystems (74). This would lead to a bV relationship, as shown in Fig. 2 (D.3). Under these conditions, more biodiverse ecosystems may actually dominate monocultures with high agrochemical inputs, from an economic value point of view.

CHALLENGES AND OPPORTUNITIES FOR FUTURE RESEARCH

Our research shows that the functional relationship between biodiversity and economic value is more variable than the well-known and often presumed positive-concave bF relationship. This enhanced complexity arises even in simplified theoretical functional relationships, as demonstrated in Table 2. Figure 4 summarizes the identified conditions driving possible bV functional forms along the three-step cascade (Fig. 1) and illustrates how far these conditions are covered by the empirical examples used in our review. The lines connecting different conditions represent the selected studies reviewed here. The large

majority of empirical studies reveal positive-concave bV relationships, while they only cover a limited number and types of conditions. The simplified roadmap reveals that, although theoretical considerations (dashed lines in Fig. 4) and single empirical observations (solid lines) give strong arguments for strictly concave and convex relationships, comprehensive studies, which capture the multitude of effects, are—to the best of our knowledge—missing. In the following section, we outline the challenges, which might explain this lack while suggesting potential next steps in science to improve the understanding of bV relationships. We structure our discussion along the conditions identified to affect bV relationships (Table 2).

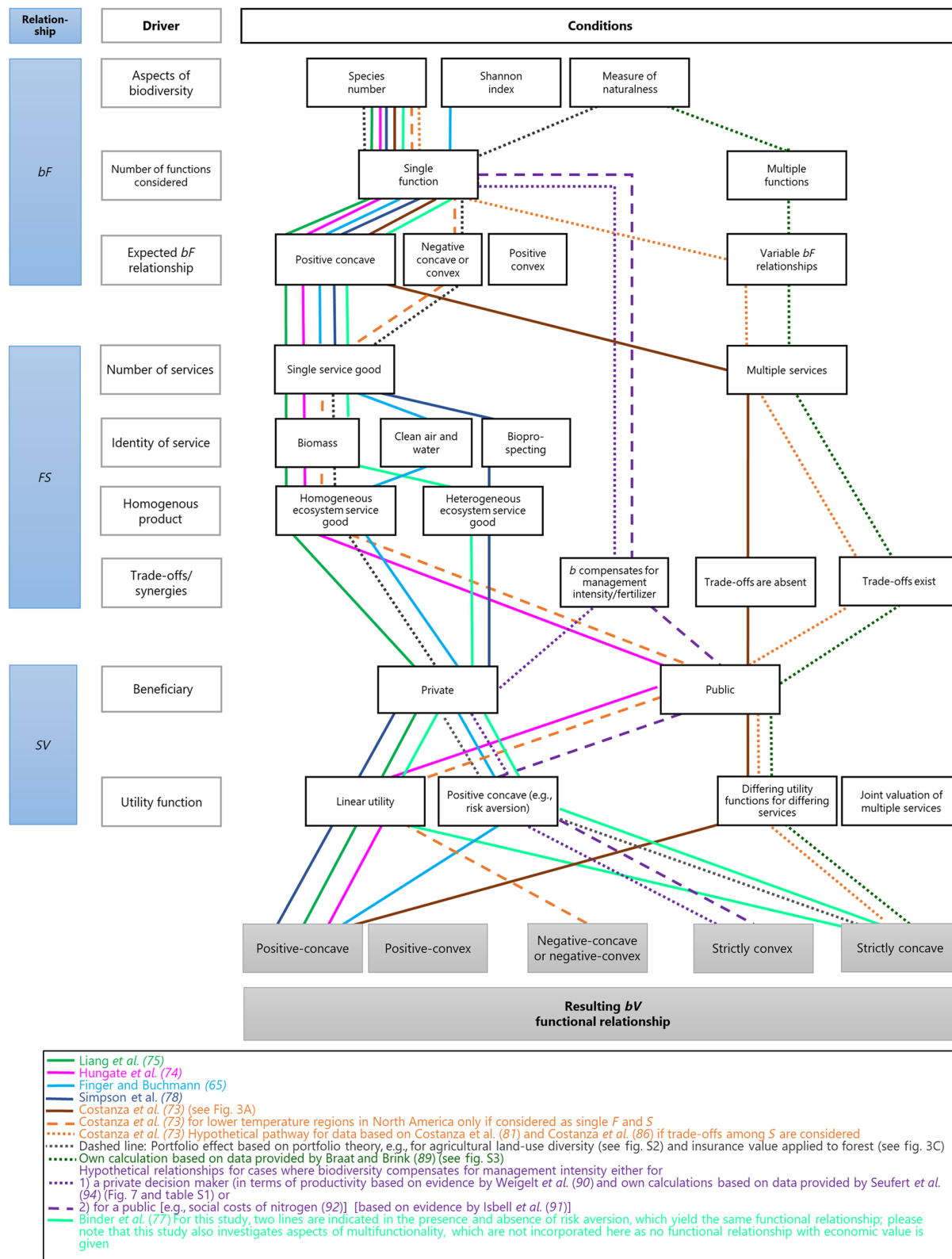
Underlying biodiversity–ecosystem function relationship

Our analysis shows that the underlying bF relationship is not the sole driver of the functional form of the relationship between biodiversity and economic values (bV) (Fig. 4 and Table 2). However, it remains the crucial foundation of bV relationships, as conceptualized in Fig. 1. A large body of literature has improved insights into the bF link during the past decade. These studies span the entire gradient of species diversity, ranging from low biodiversity levels such as in managed grassland communities consisting of a few dozen species to biodiversity-rich communities such as tropical forests. In contrast, studies investigating functional bV relationships have mostly focused on agricultural-dominated environments, thus describing a low diversity margin. This is problematic, as, for example, a typical positive-concave bV for bioprospecting arises only when considering much higher numbers of species and organisms (Fig. 2, A.3). To the best of our knowledge, bV studies covering the entire range of biodiversity levels within an ecosystem or biome are largely missing. Therefore, our review necessarily focused on bV relationships at the lower end of biodiversity levels. Future bV studies should explore a wider gradient of biodiversity levels, examining how bV shapes may be affected by the range of biodiversity levels considered. This will help develop a more nuanced and more useful view on bV relationships in science and policy.

The term biodiversity comprises a large range of concepts. While most of the examples refer to the number of species and the Shannon diversity index (Fig. 4), we have admittedly also included rather vague surrogates, such as “naturalness” (example shown in Fig. 3C) or a gradient from urban to natural landscape structures (fig. S3). We did so because these surrogates for aspects of biodiversity may be helpful for broader agricultural or forestry management decisions, for which more specific indices are not available. However, we believe that the general functional relationships are not altered by different measures of biodiversity. We have also shown that, despite very limited empirical evidence, negative bF functions may be expected under certain conditions. Accordingly, we suggest that a careful sensitivity analysis should be applied when using bV relationships for informing management decisions, which question build on the assumption of positive-concave bF . These sensitivity analyses could then estimate how changes in the underlying bF may alter bV relationships.

Type of ecosystem service considered

Our second condition along the cascade is the type of services considered and whether each species may be assumed to contribute equally to the provision of functions and the associated service. This issue could be investigated using market-based valuation methods for biodiversity. An example study is from Liang *et al.* (75), which had the primary objective of quantifying a biodiversity/productivity relationship yet also derived a positive-concave bV . Their bV relationship is based on



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Fig. 4. “Roadmap” of studies presented as examples for bV relationships. Figure orders the example studies (each study being represented by one line; see lower box for sources) by the identified drivers of functional bV relationships (boxes with gray borders) across the three-step cascade (blue boxes from top down; see Fig. 1 for abbreviations) and gives the resulting relationship (lower gray boxes). Solid lines show empirical studies, which largely follow the three-step cascade. Dashed lines reflect own considerations based on empirical and theoretical evidence (see lower box for a more detailed description). Figure is intended to show which conditions are most frequently considered or still missing in the studies reviewed here and how this may affect the resulting bV relationship.

commercial wood production to monetize the effect of tree diversity on productivity in forest ecosystems. However, they ignore the effects of highly vacillating commercial importance of different species, individual timber quality of stems, and mortality when measuring commercial value. Consideration of these differences in quality would most likely have changed the shape of the bV function, potentially altering it into a strictly concave relationship (Table 2, C.2) [e.g., (96)].

Future studies relating biodiversity with commercial value based on NPP should therefore only compare the efficient species compositions, which give the highest commercial value for each species richness level, as demonstrated by Binder *et al.* (77). Using such an approach, they demonstrate the importance of species identity and resulting product quality in grassland management. It was found that the marginal (private producer's) economic net benefit of species richness strongly declined for higher levels of biodiversity because of marginal species having higher seed costs. Their comprehensive study builds on a long-term biodiversity experiment under controlled management with differences in input costs and product quality, where quantity and prices for different species compositions are available. These comprehensive studies accounting for heterogeneous ecosystem service goods are ambitious tasks, particularly when aimed at biodiversity-rich forest ecosystems with long rotation cycles or when accounting for the uncertainty surrounding the marginal species. Despite being challenging, this research is needed for deriving robust bV relationships. Species identity might not only be important when focusing on indirect valuation of biodiversity. Jacobsen *et al.* (97) demonstrated that the type of species may also affect existence values of biodiversity, measured as WTP for habitat conservation. Hence, combining identity-specific biodiversity indices with economic valuation is an important field for future research.

Considering multiple services simultaneously

Connected to the type of services is the number of services, forming the link between biodiversity and human well-being. Scientists and policy-makers are calling for comprehensive approaches toward sustainable land use, which incorporates multiple ecosystem services and biodiversity (98). We show that considering multiple functions and services will strongly affect the bV relationship when incorporating trade-offs among services. The resulting relationship will most likely deviate from the positive-concave bV relationship observed for single ecosystem services and instead tend to be strictly concave (Table 2 and Fig. 4). In contrast, synergies among services and functions will typically not change the relationship but lead to steeper slopes. Most studies investigating trade-offs among services consider biodiversity as an additional service rather than as the foundation of ecosystem functioning and services (99, 100). A reason for this lack of studies is, first, that only few allow integration of multiple functions and/or services at the same site in a comparable time frame. This is due to the high measurement effort needed for recording multiple ecosystem functions (101). Even when these datasets are available, the problem that bF relationships are often investigated at a plot scale (see section on bF relationships) remains, while many ecosystem services require larger spatial scales, such as the landscape or regional scale (102). Trade-offs among services and the effect of management on these trade-offs may depend on the spatial scale (103). Nevertheless, the effects of biodiversity on economic value have been found to be similar across spatial scales for both grassland experiments (32) and agrobiodiversity (104). Future valuation studies should consider the landscape scale to address landscape composition and configuration

and the impact of landscape structural features on the capacity of landscapes to provide services (105). Different spatial scales of ecosystem services also affect the suitability of valuation methods and respective institutional scales (102). In our roadmap (Fig. 4), this problem of scaling may also be translated into the nature of the perspective one takes or the beneficiary one focuses on—whether valuation refers to a public or private perspective. A careful differentiation between public beneficiary and private producer perspectives is needed when selecting valuation methods and the conceptual setup of ecological-economic models, which are increasingly used to derive not only bV but also policy recommendations (98).

For analyzing multiple services and trade-offs, integrating non-market considerations are furthermore important. Improvements could encompass deriving direct and indirect values or ecological production functions for services, as demonstrated by Jonsson *et al.* (106), for biological control services in agricultural landscapes. We also see much potential for valuing ecosystem services based on stated preference or production function methods. Choice experiments could even help value various biodiversity-dependent services simultaneously. A consistent use of methods is important not only to derive scientifically sound bV relationships but also to identify adequate governance instruments for each perspective (102). For a more specific discussion of valuation methods—which is not our primary focus here—we refer the reader to more specific literature on this topic (3, 15).

Effect of synthetic inputs and ecological replacement

Ecological intensification is discussed as a key strategy to sustain agricultural production while minimizing adverse effects on the environment. Kleijn *et al.* (95) conceptualize the role of biodiversity in this concept through two pathways: first, to use biodiversity to complement external inputs, thus increasing agricultural productivity, or second, to replace artificial inputs while holding yield constant. Our theoretical analysis shows that substitution between biodiversity and synthetic inputs may lead to strictly convex relationships. This finding gives further support to the empirical observation by Kleijn *et al.* (95) that practical uptake of ecological intensification is still very limited, despite scientific evidence on its benefits. The strictly convex relationship conceptualized here may explain this apparent paradox, in that the initial decline in economic value (left end in Fig. 2D) may drive farm decisions, while science tends to perceive and promote the increase at higher biodiversity levels (Fig. 2D, left end).

With the latter statement being a rather bold hypothesis, it underlines the importance of biodiversity as a replacement for agrochemicals and the need for proper integration of these considerations into economic valuation studies. The contribution of biodiversity to the production function of a service may be valued as well as the avoidance of costs by reducing inputs, such as fertilizer, irrigation, or pesticides. For assessing the effects of ecological intensification, it is again crucial to distinguish between private producers and public beneficiaries, represented by methods of either private or social cost benefit analysis (95). In our theoretical example, we find that considering social costs and benefits enhances the functional relationship of a strictly convex relationship. A better integration of these relationships into decision-making would consequently be desirable.

Selection of appropriate utility function

A further aspect to be improved is the use of specific utility functions to link changes in ecosystem service supply to changes in human well-being and choices. We found that using a positive-concave utility function

instead of linear utility functions strongly affects the bV relationship. Both negative and positive bV relationships may then turn into strictly concave bV relationships.

The selection of utility function(s) is also important when considering how the utility of a group of different stakeholders is influenced by the provision of ecosystem services. This is required when valuing multiple, mostly public ecosystem service goods, all being affected by aspects of biodiversity. Problems may, in part, be overcome by means of group deliberation to improve the aggregation of preferences among various stakeholders (107). However, it is generally difficult to arrive at a consistent collective preference scale. Arrow (108) has shown that this may be theoretically impossible. While one could accept summing individual utilities as a decision criterion, Rawls (109) has suggested to arrange inequalities in a society in a way that the worst-off people will benefit most. Other social welfare functions can be used for aggregation of economic values. Improved use of utility functions in ecological valuation studies is therefore an essential interface to enable the cooperation between the disciplines of ecology and economics. Testing and communicating the effect of different utility functions on derived bV relationships should become a standard procedure. Last, we note that people may well derive a different direct value from a gain in biodiversity compared to an equivalent loss for reasons of loss aversion. This behavioral phenomenon suggests that humans systematically rate losses higher than gains. The degree of this difference goes beyond that explained by diminishing marginal utility. If loss aversion describes preferences for biodiversity, then people will be willing to pay significantly more to prevent a given decline in species richness, say, compared with their WTP for equivalent increases in species richness.

Incorporating uncertainties and future options

Our study underlines the call for better integration of uncertainty in ecological-economic research. We find that including trade-offs between risk and return may imply a strictly concave bV relationship. However, uncertainty is also involved in estimating ecosystem service values and in how these are influenced by biodiversity. We found only few studies that account for these uncertainties. To do so, portfolio models could be applied, which are able to simulate species or land use and land cover diversification and their consequences at ecosystem or landscape scale (77, 110). In addition, addressing option values associated with biodiversity would be an interesting topic for further research. This includes the linkage of biodiversity to real options theory, for example, in the context of invasive species control (111). We have shown that research on flexibility aspects supported by biodiversity, in the sense of option values [i.e., (15, 68)], has potential to advance the understanding of the contribution of biodiversity to human well-being.

CONCLUSIONS FOR SCIENCE AND POLICY

Our analysis reveals that bV relationships are more complex than often assumed. Despite the current scientific consensus on positive-concave bF relationships, one cannot conclude that bV relationships are always of the same shape. This is because the shapes of the additional functions/services and services/economic value relationships modify, alter, or even invert the shape of the underlying bF relationship. Consequently, maximizing biodiversity at the ecosystem level will not maximize economic value in most cases. This is particularly true when considering trade-offs between different services or between economic returns and risks. Empirical and theoretical evidence for strictly concave

or strictly convex bV relationships does not, however, undermine the idea of the importance of the value of biodiversity for human welfare. Strictly concave relationships highlight the importance of maintaining biodiversity at or increasing biodiversity to moderate levels. Incorporating these bV relationships into land-use planning could support active use of positive bF relationships in managed ecosystems. For example, these results could provide important economic arguments to reduce fertilizer and pesticide input in a transition to more diverse, mixed cropping and forestry systems or agroforestry. A better representation of biodiversity in land-use planning could thus support both enhanced human well-being and the protection of megadiverse natural ecosystems.

In this study, we focus on studies that take the most common view of anthropocentric and instrumental values (14) more commonly implemented by government departments as well as agencies such as the World Bank (4). This interpretation of bV relationships not only does allow us to build comparable functional relationships but also has high relevance for political decision-makers. Nevertheless, we acknowledge that a comprehensive solution for nature conservation will inherently depend on pluralistic and integrated valuation approaches, which incorporate diverse worldviews and understandings of value (2, 55).

In conclusion, carefully accounting for the multifaceted interdependencies between biodiversity and economic value will improve the future economic valuation of biodiversity. Calculation of economic values of services helps raise awareness of the importance of biodiversity but will only improve decision-making if the actual contribution of biodiversity to the economic value flows is made explicit and context specific.

SUPPLEMENTARY MATERIALS

Supplementary material for this article is available at <http://advances.sciencemag.org/cgi/content/full/6/5/eaax7712/DC1>

Supplementary Methods

Fig. S1. Schematic demand and supply curves for a marketable and nonmarketable ecosystem service (5).

Fig. S2. A decreasing standard deviation and expected economic return of a portfolio consisting of crops when successively adding further crop options.

Fig. S3. Theoretic individual and aggregated bV relationships following Braat and ten Brink (89).

Fig. S4. Impact of cropping systems and N input on agricultural yield.

Table S1. Statistical analysis of the effect of multicropping on agricultural yield when N input is considered as independent variable.

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