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REVIEW AND SYNTHESIS

From biodiversity to health: Quantifying the impact of diverse ecosystems on human well-being

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Abstract

1. Ample evidence suggests positive effects of species diversity on ecosystem functioning and services in natural and agricultural landscapes. Less obvious and even contested are the effects of such diversity on human well-being. This state of art partly stems from methodological difficulties to evaluate and quantify these effects and imprecise conceptual frameworks.
2. Here we propose a conceptual framework that links different aspects of diversity, particularly species and genetic richness, to ecosystem functioning, ecosystem services and disservices, and different aspects of well-being. We review current approaches for the study of diversity–well-being relationships and identify shortcomings and principle obstacles, mainly stemming from theoretical premises that are too imprecise.
3. We discuss five basic methodological approaches to link diversity to well-being: matrix models, indirect inference, Price partitioning, structural equation modelling, and environmental inference.
4. We call for a stricter terminology with respect to the different aspects of functioning, multifunctionality and well-being and highlight the need to evaluate each step in the different pathways from diversity to well-being. A full understanding of ecological constraints on human well-being requires consideration of trade-offs in diversity effects, of contrasting perceptions of well-being, and of ecosystem disservices. We also call for appropriate long-term socio-ecological

research platforms to gather relevant data about ecosystem functioning and well-being across space and time.

KEYWORDS
diversity, ecosystem disservices, ecosystem services, matrix models, multifunctionality, statistical inference, structural equation modelling

1 | INTRODUCTION

During the past 30 years, ecologists have amounted strong evidence that, on average, more diverse, that means more species rich, natural ecosystems and those modified by humans are functionally and compositionally more stable (e.g. Loreau & de Mazancourt, 2013; Tilman et al., 2006), resilient (e.g. Dell et al., 2019; Elmqvist et al., 2003), and robust against disturbances (e.g. MacDougall et al., 2013). Theoretical and empirical evidence predicts that high taxonomical and functional diversity particularly increase energy transfer (Barnes et al., 2018; Buzhdygan et al., 2020), nutrient cycling (Roscher et al., 2004), production (Hector et al., 2010; Huang et al., 2018) and food web stability (Zhao et al., 2019) and, consequently, ecosystem functioning (Hooper et al., 2005; Weisser et al., 2017).

Closely related to ecological functionality is the widely used concept of ecosystem services (Daily et al., 1997) stemming from the notion that part of these ecosystem functions supported by biodiversity directly benefits human well-being, particularly human health (Lee et al., 2021; MA, 2005; WHO, 2015). Human well-being is a very broad concept that has been used interchangeable with personal happiness, quality of life and health, but also more generally with human welfare, intact social bonds and human rights (Clark, 2014). Some of these concepts are difficult to quantify and therefore might not allow for a projection onto environmental diversity. Therefore, we here follow Summers et al. (2012) and refer to physical, mental and cultural well-being including four quantifiable elements: basic needs, economic needs, environmental needs and subjective happiness. Intuitively, these elements should require a natural and productive environment. Consequently, we focus on agriculturally modified landscapes.

Important directly quantifiable ecosystem services include food production, air and water cleaning, water retention, carbon sequestration, climate regulation and soil fertility (Brondizio et al., 2019; Daily et al., 1997; Montanarella et al., 2018). Less apparent but not less important are, for instance, pest control, delivery of genetic material and medically important secondary metabolites, pollination, natural nutrient supply, stabilization of the immune system or pedogenesis (de Groot et al., 2002; Rook, 2013). Consequently, several authors have made a causal link between diversity, ecological functioning, ecosystem services and human well-being, the latter including health status (e.g. Aerts et al., 2018; Kilpatrick et al., 2017; Lovell et al., 2014; MA, 2005; Methorst et al., 2021). The WHO report (WHO, 2015) and Marselle et al. (2019, 2021) have reviewed the state of the art and outlined general frameworks and study directions linking some of these aspects.

Increasing work has been devoted to cultural ecosystem services and human well-being (reviewed in Jax et al., 2018 and Kosanic & Petzold, 2020). Cultural ecosystem services refer to the non-material benefits that directly influence the life quality (Plieninger et al., 2013). Different classifications of these services have been proposed, but all of them highlight recreation and ecotourism, cultural heritage, education and spiritual values as being most important (e.g. Plieninger et al., 2013). An assessment of these cultural ecosystem services requires a toolbox from the social science including participatory methods and accessibility assessment (Cheng et al., 2019; Crouzat et al., 2022; Montes-Pulido & Forero, 2021).

The mentioned work on ecosystem services demonstrates how much of our current view about the impact of biodiversity on human well-being is still based on broad generalizations and common belief and how little we know about the strength of specific biodiversity–well-being relationships and possible trade-off between these relationships. Additionally, the question how to quantify the relationships between biodiversity and human well-being has gained too little attention (Levy et al., 2012), seemingly due to spatio-temporal scale issues, as well as different ways of measuring diversity and well-being that hinder cross study comparisons and quantitative meta-analyses, making this research field still predominantly case study orientated (Aerts et al., 2018; Lee et al., 2021).

Here, we aim to address this knowledge gap considering the strength of specific biodiversity–well-being relationships and possible trade-offs between then. To accomplish this goal and to overcome limitations in the analytical approaches, we focus on the need to match qualitative and quantitative approaches to relate biodiversity, ecosystem functioning, and human well-being. For this purpose, we present five advanced multivariate data analytical methods. We argue that any inference of the links between diversity and human well-being needs sufficiently flexible and multidimensional modelling approaches. Bi-variate comparisons of measures of diversity and human health status appear to be less promising while not accounting for the inherent complex nature of diversity effects on ecosystem functioning and well-being.

2 | KEY PATHWAYS FROM DIVERSITY TO ECOSYSTEM FUNCTIONING

2.1 | A conceptual framework

Rendón et al. (2019), Marselle et al. (2021), and de la Riva et al. (2022) previously outlined major positive effects of ecosystem functioning on humans. To quantify these effects, we need to disentangle the many facets of functioning but also the complex direct and indirect relationships between environmental changes and health issues. For this task, we introduce a framework that incorporates the many aspects of diversity across levels of differentiation and differentiates between constituent diversity (genes, species, guilds) and systems diversity (functional diversity, interaction network complexity) (Figure 1). Both constituent and systems diversity stabilize ecological interactions (Tilman et al., 1998) and increase system robustness and resilience (Landi et al., 2018; Oliver et al., 2015). In this respect, we see ecosystem multifunctionality (Manning et al., 2018) as an integrative concept over multiple important single aspects of systems diversity. In our view, the ecological multifunctionality concept lacks developed counterparts with respect to ecosystem services and the different aspects of well-being. Fagerholm et al. (2020) application of a multifunctional landscape concept to well-being might be seen as a step in this direction.

Multifunctionality refers to the ability of ecosystems to provide a multitude of functions and ecosystem services (Manning et al., 2018). Within this framework supposed positive ecosystem effects on human well-being should include more than a single functional category to be conclusive (e.g. timber production, recreation, and soil formation might cause positive and negative well-being effects depending on the social perspective). Consequently, the different well-being and functioning categories mentioned in Figure 1 are not independent and an integrative inference would need to include the many trade-offs between these categories. In this respect, the multifunctionality concept can be seen as a holistic approach to such inference. We note that the framework outlined in Figure 1, in principle, refers also to crop plant and livestock health. While much work has been devoted to the negative impacts of livestock on diversity, the possible positive effects of diversity and multifunctionality on plant and animal health have not received sufficient attention (Herrero et al., 2015).

We assume that four major drivers of global change (change in land use, climate change, land degradation and pollution) determine constituent and systems diversity, influence the levels of productive and regulatory ecosystem functions (Brondizio et al., 2019; Díaz et al., 2018) and might directly affect human well-being (Figure 1). Along these relationships we will discuss quantification issues and possible pitfalls in the assessment of biodiversity impacts on human well-being. This framework also recognizes the direct effects of environmental changes on human health, such as urbanization or pollution, not being only mediated by biodiversity (Figure 1). We do not differentiate among the many aspects of human well-being as this would go far beyond the scope of the present methodology orientated revision (cf. Summers et al., 2012). But we caution that we should not generalize diversity–well-being relationships and possible recommendations from single studies or from the study of single elements of well-being alone.

The ecosystem service concept includes the possibility that natural ecosystems might also provide disservices (Gutierrez-Arellano & Mulligan, 2018; Shackleton et al., 2016), including harmful organisms. Ecosystem services and disservices often covary as they are indirectly related and therefore have to be seen in terms of synergies and trade-offs with the consequence that land use may alter the strength of these relationships (Birkhofer et al., 2015, 2021) and that intact ecosystems might not only have a positive effect on human well-being. Current reviews on ecosystem services have not fully recognized these trade-offs (Marselle et al., 2021; Rendón et al., 2019). Any assessment of diversity–well-being relationships needs first to account for individual positive and negative relationships and then to quantify the resulting net effects.

It is now generally accepted that the aspects of constituent diversity are positively correlated with ecosystem productivity (Tilman et al., 2012) and element cycling (Hättenschwiler

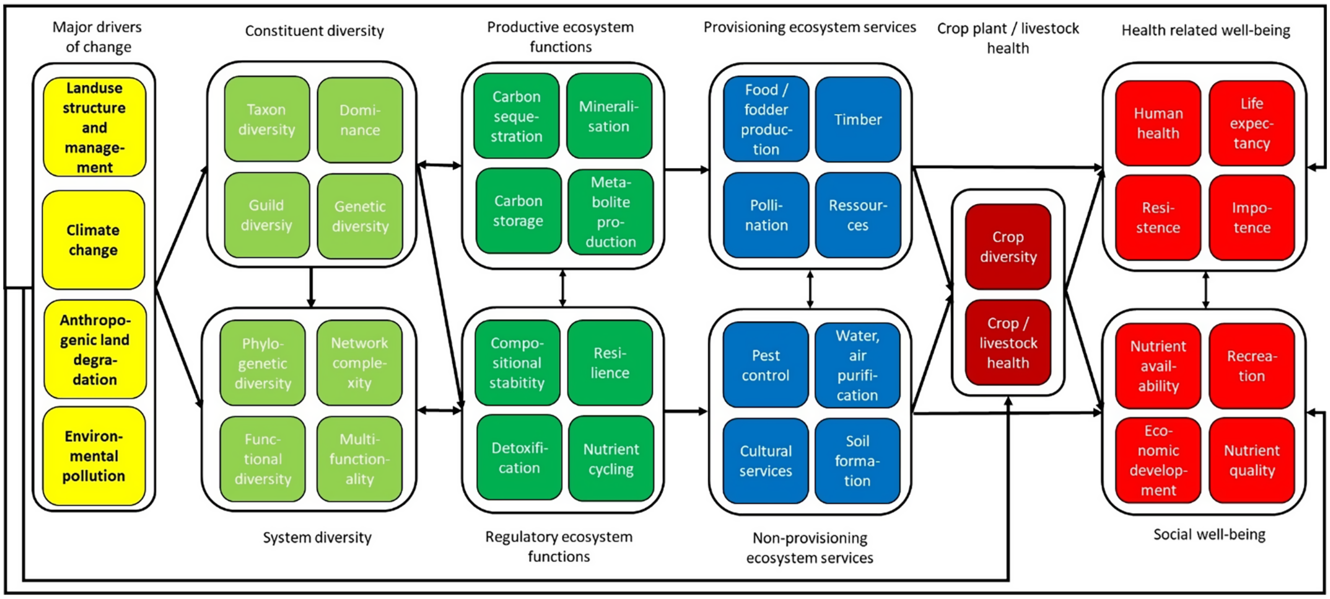


FIGURE 1 From major drivers of environmental change to human health related well-being.

et al., 2005) and, therefore, ecosystem integrity (Hansen et al., 2021). However, the question whether systems diversity, particularly food web complexity and functional diversity, positively correlates with the various aspects of ecosystem functioning is still controversially discussed despite strong claims in favour (e.g. Balvanera et al., 2006; Bastian, 2013). For instance, Díaz et al. (2007) and Cadotte et al. (2011) demonstrated how systems diversity, particularly functional diversity and species dominances boost ecosystem functions. In turn, Sullivan et al. (2017) failed to find any correlation between functional diversity and carbon storage in tropical habitats. Based on bee flower visitation data, Kleijn et al. (2015) cautioned that pollination efficacy alone is a weak argument in favour of bee protection. Apparently, there are no universal causal relationships and case-specific relationships might vary considerably in direction depending on scale, study system, and geographic area. This calls for case specific assessments of diversity–ecosystem functioning relationships and should caution us in terms of generalizations. Consequently, any tracing of pathways from ecological functioning to human well-being needs quantifiable relationships at each stage along the chain. The starting hypothesis that diverse ecosystems increase human well-being is in fact an amalgam of several, not necessarily coherent, assumptions about causal relationships along a multitude of single dependencies that form causal chains. These chains might not always be linear but will often contain bi- or even multidirectional causal relationships. Consequently, we need appropriate modelling techniques that are able to disentangle such complex causal relationships.

Well-being as a quality of human life also needs to be precisely defined as ecosystem functioning and services do not apply to all people equally and may even cause conflicting opinions (Felipe-Lucia et al., 2015, 2022). High expressions of provisioning ecosystem services are customer specific and the mix of these services might include a trade-off with unknown effects on biodiversity and ecosystem functioning. For instance, the ecosystem services that soils provide in different major ecosystems (e.g. urban, agricultural, natural) may be valued very differently depending on the perception and priorities of end users. While urban citizens may prefer opportunities for soils to support construction (urban sprawl), farmers prioritize food production and conservation practitioners focus on the protection of biodiversity, which results in competing priorities for ecosystem service provision from the same land (Setälä et al., 2014). So far, trade-offs in different dimensions of well-being have not sufficiently been studied (e.g. Lapointe et al., 2021; Santos-Martín et al., 2013, for indirect perception-based inferences), but may have important effects on the assessment of diversity–well-being relationships and the respective management decisions. We propose to apply the multifunctionality concept of community ecology and its associated measures (Manning et al., 2018) also to the different dimensions of well-being to obtain a coherent quantification of well-being across its different elements, by this accounting for possible trade-offs.

3 | QUANTIFYING FUNCTIONALITY AND WELL-BEING

3.1 | Approaches to ecosystem comparisons

Diversity–well-being relationships might be studied from very different perspectives. In Figure 2, we exemplify six basic diversity–disturbance combinations and the resulting ways for comparison. For convenience, we use the term disturbance to quantify the degree to which a system deviates from being natural. Many studies have asked whether (often more diverse) natural ecosystems foster well-being more than (mainly less diverse) anthropogenic systems (Balmford & Bond, 2005; MA, 2005; Summers et al., 2012). Such an approach does not directly answer to the question of whether diversity itself improves well-being. It studies the combined effects of diversity and the degree of anthropogenic disturbance on well-being. In fact, this cautionary note refers to all studies that compare diversity and well-being across different types of ecosystem and also across habitats of the same type influenced by different environmental conditions. For example, anthropogenic environments of higher and lower diversity might differently impact well-being. Well-being then jointly results from a diversity effect and the effect of difference between the ecosystem types used for comparison. Consequently, we mainly assess the degree of change in land-use or

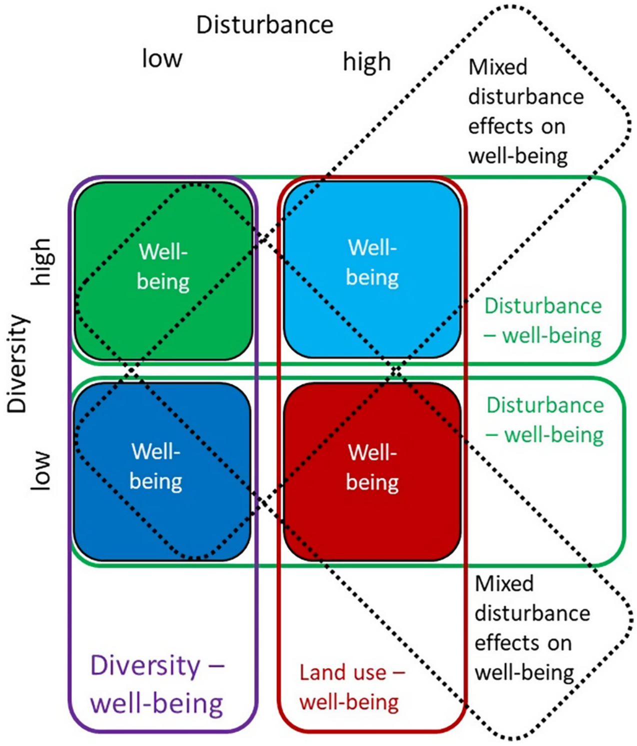


FIGURE 2 Six possible types of combinations (rectangles) of ecosystems with lower and higher diversity and degree of disturbance (naturalness) to study the impact on well-being. The impact of diversity only (diversity–well-being relationship) is best studied comparing natural ecosystems with low and high diversity.

landscape reshaping on well-being rather than the mechanistic link between diversity and well-being (Figure 2).

Comparisons of disturbed and undisturbed species rich and poor systems might be able to infer the effect of disturbance on well-being. This is an important task in its own right and a major issue in agricultural landscapes, where the total species richness of many taxa is still high and close to the undisturbed state despite of major changes in land use. This approach would only tell about diversity effects on well-being if we could partition the effects of species richness from the disturbance effects.

We argue that for a direct inference of diversity effects on well-being we need to look at ecological systems and asks whether differences in diversity of these systems differently influence ecosystem services and human well-being (Figure 2). We need to combine these approaches in a multivariate analysis of diversity–disturbance–well-being relationships although unequivocal interpretation still might be challenging. Importantly, all these approaches have a spatial and temporal dimension and we might particularly differentiate between local and landscape scale diversity effects on well-being (Methorst et al., 2021), as well as short- and long-term effects (Qiu & Cardinale, 2020). These different approaches to compare ecosystems of different diversity and disturbance levels have not always been clearly separated (e.g. Haynes-Young & Potschin, 2010; Marselle et al., 2021).

3.2 | Statistical issues

In the environmental and also the social sciences, statistical inference is generally based on Pearson-Neyman and Bayesian frameworks. These do not test empirical hypotheses as required by classical models of scientific inference (Kuhn, 1966) but try to reject theoretical constructs (the null assumptions or statistical standards) in favour of our hypotheses (Lehman & Romano, 2005). These approaches work well for simple cause–effect relationships with intermediate numbers of samples. However, today's ecological, medical and sociological datasets often contain thousands or even tens of thousands of single data, allowing for more than one possible statistical standard, and cover complex variable relationships. At such sample sizes and levels of complexity classical statistical inference with associated significance levels break down while too often pointing to high significance although in fact not having any real impact (Burnham & Anderson, 2002; Lehman & Romano, 2005; van der Laan & Hsu, 2010). Reliance on significance levels only might heavily bias our impression on the relative importance of different well-being drivers when using the results of meta-analytical studies. It has consequences for the detection of the influences of diversity and ecosystem functions on human well-being. Therefore, we emphasize the need to rely on effect sizes instead of significances to quantify relationships. In most cases these will be estimates of the proportion of explained variability in the response variable. Importantly, we use the term 'quantitative' in a broad sense as any quantitative approach might also cover qualitative inference using appropriately coded categories of well-being and ecological functioning (e.g. positive versus negative effects or answers in participatory research).

Below, we discuss methods for the assessment of diversity–well-being relationships and present five approaches suited to deal with quantitative and appropriately coded qualitative data. These approaches include structural equation modelling of the drivers of well-being, matrix models to link sets of variables, price partitioning for the study of temporal or spatial change in functioning, the integrative analysis of multiple ecosystem functions, and environmental modelling. We choose these methods from the multitude of available statistical tools as each of them tackles a different question based on specific data structures relevant to the functional diversity-human well-being relationships. In this respect, they can be seen as being complementary. We do not claim this set of approaches to be exhaustive. Our choice was guided by the potential for broad application in combination with ecological, economic and sociological data.

3.3 | Assessing diversity–well-being relationship

The detection of biodiversity effects on human well-being must not rely on a simple bivariate analysis (Figure 1). Diversity is mediated by consecutive steps of influence and any appropriate analysis of these influences needs to account for a chain of relationships, where each step has to be quantified appropriately. In Figure 3, we develop a respective framework and indicate important single steps of this chain with respective examples of quantification. Ideally, these steps should be applied in the comparisons outlined in Figure 2 and can be simplified to environment ↔ diversity ↔ community functioning ↔ ecosystem services ↔ well-being, where the double arrows indicate possible mutual relationships. We note that in many cases not all data of Figure 3 will be available at the cost of reduced power of the argument regarding diversity–well-being effects.

The shortest way from local species diversity to human well-being is a three-step pathway and includes community functioning and important ecosystem services like water and soil purification and formation (Figure 3). Therefore, this chain appears to be most promising for any respective inference. Other analyses are more indirect and include community functioning steps, and either ecosystem services or plant and animal well-being (Figure 3). In all cases, we might wish to account for landscape structure, land use, and, casually, ecological history to proper assess the focal diversity status.

Diversity might be related directly to a focal aspect of human health in a bivariate comparison. For instance, Methorst et al. (2021) used bivariate regressions to link diversity and environmental characteristics to measures of human well-being and found particularly bird species richness and recreation access to correlate positively with well-being. In a participatory study, Bryce et al. (2016) used questionnaires to directly relate biodiversity to cultural well-being. However, it remains unclear, as cautioned by the authors themselves, whether bird richness was the ultimate cause of well-being or only a proximate reason influenced by some hidden general factor such

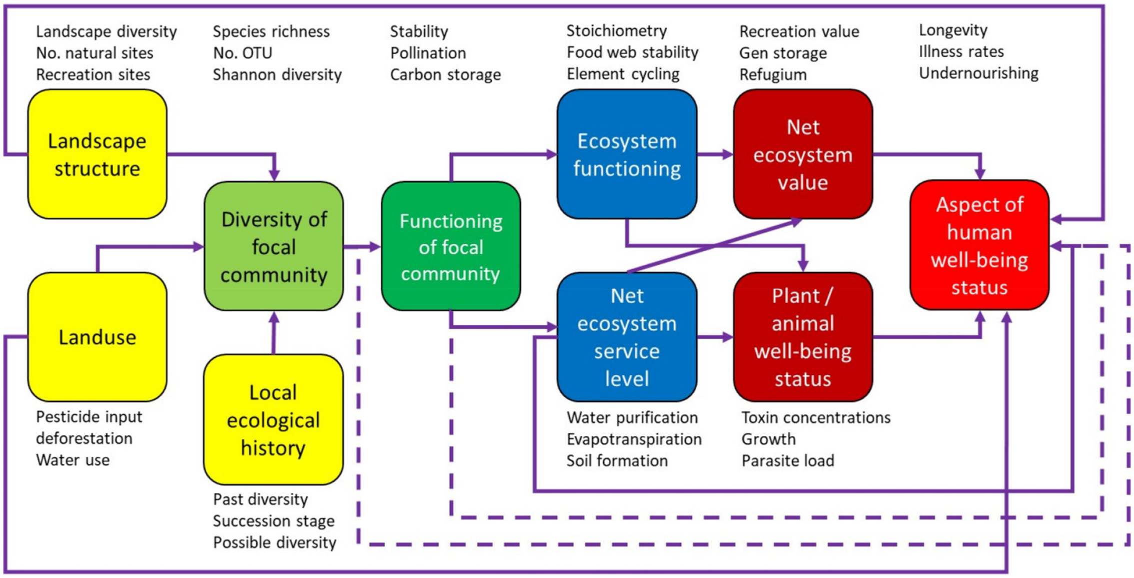


FIGURE 3 Pathways from landscape use and community structure to human well-being with examples of possible ways of quantification. Solid arrows mark proposed causal links. Dashed arrows from diversity and community functioning to human well-being denote links that cannot be unequivocally confirmed using correlative analysis.

as the availability of green spaces or fresh air. This case study highlights some difficulties particularly with the assessment of cultural well-being, not only when based on participatory studies. Similarly, Hummel et al. (2019) drew attention to the difficulties in applying ecosystem service concepts to protected areas. Hidden factors and traditions might also bias the results. For instance, in a recent participatory assessment of cultural well-being and forest conservation Nzau et al. (2022) showed how tradition and social status differently influence the perception of ecosystem values of Kenyan rural people. Further, correlative inferences do not inform us about causal relationships as a number of covariates listed in Figures 1 and 2 might influence both variables in unknown ways, both in identical or opposite directions. We would need to compare a manifold of single bivariate patterns or multiple partial analyses obtained in different configurations of habitat and ecosystem functioning to rule out these covariates. These data might stem from controlled experiments, empirical samples or participatory studies.

Inference of the diversity–well-being relationship might be conducted by a correlative approach including linear or nonlinear additive models (general linear models *glm*, ANOVA, generalized additive models *gam*; Zuur et al., 2009). These approaches have apparent or hidden shortcomings. An apparent point of caution is the equiprobable random standard most regression models are based on. Even when using non-normal error distributions, the null assumption for independence implies zero covariance and regression slope. These expectations are in many ecologically realistic situations not justified making inference of statistical significance of the model parameters questionable. A well-known example involves two variables, where one is constraint by the second (Nee et al., 2005). In this case both variables, even if being independent random numbers, will positively correlate. With respect to ecosystem functioning measures, we might imagine a food web of several trophic levels, where the abundances and therefore also the diversity of higher levels are constrained by the abundances in the lower levels. In this case, the proper null assumption of non-independence will be a function of the degree of constrain. Furthermore, measurement method might determine the type of constraint and thus influence our statistical inference. If human and animal/plant well-being are quantified by similar metrics, one metric might have values that are always within the second one. In this case both automatically become positively correlated. Standard regression analysis will return inflated levels of significance for the positive relationship between both variables and therefore erroneously assess the impact of animal/plant well-being on human health.

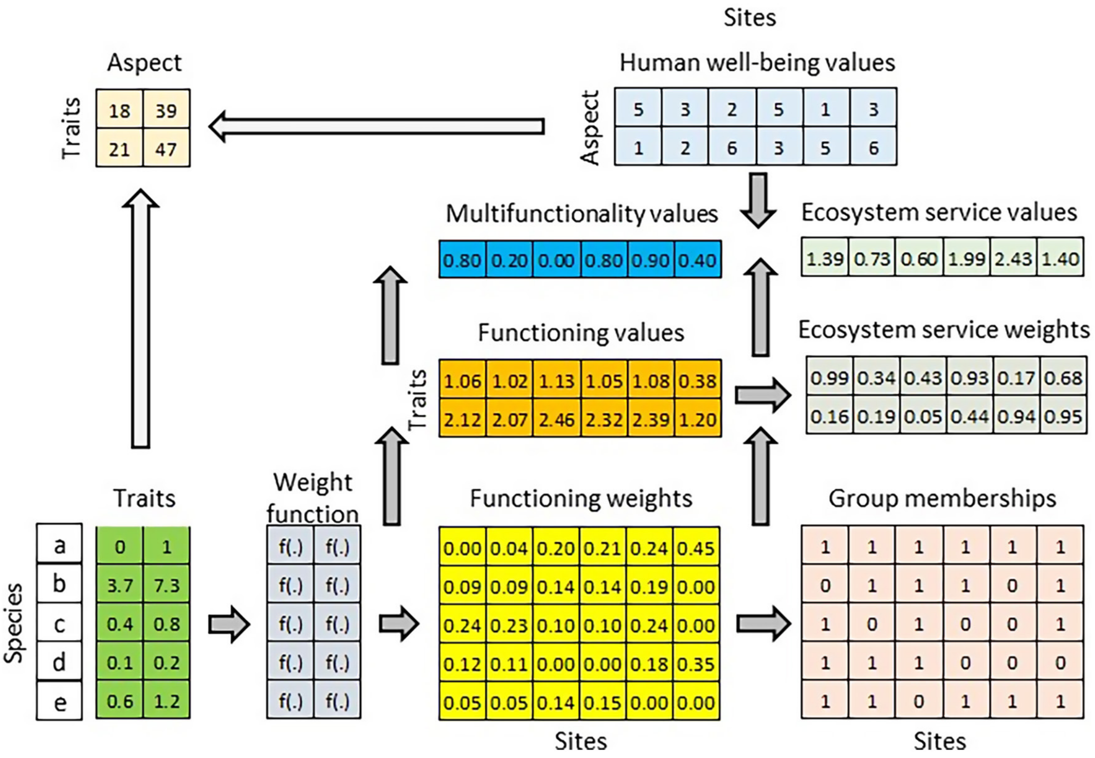
The pathway from diversity to human well-being contains apparent and possible latent variables, the latter in the form of covariates to each of the factors shown in Figures 1 and 2. The covariates include human influences on each of the steps and therefore causal loops as well as inherent constraints on each variable. For instance, human well-being has an impact on animal health and ecosystem functioning (Naeem et al., 2009). The level of ecosystem functioning impacts local diversity, which is related to human health (Newbold et al., 2019). These causal loops make any application of one-directional linear modelling like *glm*, *gam*, or matrix models less interpretable than it seems. Therefore, we argue in favour of statistical models that are able to handle such bidirectional dependencies. Particularly, different path analytical approaches are able to evaluate the likelihood of causal pathways.

In both, bi- and multivariate regression approaches, high sample sizes inevitably increase type II error levels (Burnham & Anderson, 2002). A five-step regression chain or a five-level path analysis network from diversity to human well-being with at least 11 degrees of freedom would need more than 500 single and independent data points (50 for each degree of freedom) for the detection of at least moderate effect sizes (Zuur et al., 2009). To support the argument of positive effects of high diversity on health, the regression analysis would need to be significant at each of the five steps. Importantly, effect sizes (EF) of such a chain act multiplicatively. Therefore, in case of average moderate single effect sizes of, for instance, 50% the final estimate for the impact of diversity on human well-being will be $EF = 0.5^5 = 0.03 \equiv 3\%$. For the three-step chain we reach in a final $EF = 0.5^3 = 0.13 \equiv 13\%$. In any case, we need to have a manifold of independent studies to corroborate the hypothesis of a positive impact of diversity on human well-being.

3.4 | A matrix approach to inference

In community ecology multiple matrix approaches for assessing community assembly from information on species traits, phylogenetic relatedness, interaction dynamics, and environmental filtering are well introduced (Dray & Legendre, 2008; ter Braak, 2017; Ulrich et al., 2018). Fourth corner and related correspondence analytical tools allow for a direct mapping of species traits on environmental data via a link matrix, typically containing species abundances, presence–absence biomass data (Dolédec et al., 1996), or weighing factors like species interaction strength (Ulrich et al., 2014). In Figure 4, we propose a multiple matrix approach to the study of the diversity—well-being relationship with entry data able to parameterize the analytical steps identified in Figure 3. Importantly, any qualitative or quantitative (coded) data might be used as matrix entries.

Fourth corner statistics use inner matrix multiplication to link a species × trait matrix **T** with an environmental variable × site matrix via a species × site link matrix **M**. In the present case this might be a matrix containing aspects of human well-being (Figure 4). The result is a trait × aspect matrix where entries are respective effect sizes (correlations in cases of Z-transformed values and a presence–absence link matrix) of the dependences of trait expression and well-being. Statistical testing comes from appropriate randomization approaches. We note that in case of linear relationships and an abundance matrix **M** the inner product $\mathbf{T}^{\mathrm{T}}\mathbf{M}$ provides total trait expressions at each site (Figure 4), from which we can calculate the site specific degrees of multifunctionality (Manning et al., 2018). Unfortunately, individual trait expressions tend to vary across sites in dependences on environmental factors and on species interactions making direct inferences of ecosystem functioning and trait–well-being correlations challenging (de Bello et al., 2011). Therefore, we will often need habitat specific link functions for the trait–environment relationship (Figure 4). This step seems to be crucial as intraspecific trait variability and nonlinear environmental trait scaling might heavily influence estimates of ecosystem functioning and multifunctionality (Des Roches et al., 2018; Wong &



Aspect (Traits)

18	39
21	47

Human well-being values (Aspect × Sites)

5	3	2	5	1	3
1	2	6	3	5	6

Multifunctionality values

0.80	0.20	0.00	0.80	0.90	0.40

Ecosystem service values

1.39	0.73	0.60	1.99	2.43	1.40

Functioning values (Traits)

1.06	1.02	1.13	1.05	1.08	0.38
2.12	2.07	2.46	2.32	2.39	1.20

Ecosystem service weights

0.99	0.34	0.43	0.93	0.17	0.68
0.16	0.19	0.05	0.44	0.94	0.95

Traits (Species)

a	0	1
b	3.7	7.3
c	0.4	0.8
d	0.1	0.2
e	0.6	1.2

Weight function

f(.)	f(.)
f(.)	f(.)
f(.)	f(.)
f(.)	f(.)
f(.)	f(.)

Functioning weights (Sites)

0.00	0.04	0.20	0.21	0.24	0.45
0.09	0.09	0.14	0.14	0.19	0.00
0.24	0.23	0.10	0.10	0.24	0.00
0.12	0.11	0.00	0.00	0.18	0.35
0.05	0.05	0.14	0.15	0.00	0.00

Group memberships (Sites)

1	1	1	1	1	1
0	1	1	1	0	1
1	0	1	0	0	1
1	1	1	0	0	0
1	1	0	1	1	1

FIGURE 4 A matrix model to exemplify the data necessary for a proposed analysis of the diversity well-being relationship: three species (a–e) based matrices: (a) species × traits, (b) species × functioning weights across sites, (c) species × group membership across sites and a matrix containing values of different aspects of human well-being across study sites. Species trait expression is generally depending on the environment and therefore needs a link function *f*(.) to be linked to functioning weights. Matrix operations allow for estimations of functionality and ecosystem service values.

Carmona, 2021). Recently, Sarker et al. (2021) demonstrated the validity of this approach comparing a variety of nonlinear link functions and models to calculate mangrove primary production from variable tree trait expressions. Similar approaches should be used to assess ecosystem service values from trait compositions (Figure 4). The resulting function values might then be correlated with some quantification of human well-being, if appropriate again using link functions (Manning et al., 2018).

In a different approach we might wish to define ecological groups or functional guild using a matrix of guild membership when linking traits with functioning weights (for instance, abundance or biomass values). Combined with respective link functions (weights) as before this approach provides function values and ecosystem service contributions for focal groups/guilds. This allows for an assessment of the contribution of these groups/guilds to observed human well-being levels (Figure 4).

3.5 | Price partitioning

Despite recent critiques (Pillai & Gouhier, 2019; van Veelen, 2020) a promising approach to link changes in well-being to diversity measured by species richness or functional diversity implies the use of price partitioning. The price equation of evolutionary biology applied to ecological communities (Fox, 2006; Loreau & Hector, 2001) states that the total change in some character value in a community might be partitioned into additive parts containing the contribution of community diversity and the covariance of trait values and composition. Ulrich et al. (2022) introduced a new partition that includes also the effects of changes in total community abundances. When applied to the change in the value of a focal community function or of an ecosystem service this partitioning can be simplified into a three-partition solution (Ulrich et al., 2022)

$$\Delta F = \overline{w_A}\,\Delta S + a\overline{\Delta p} + b\overline{F_A}\,\Delta N, \tag{1}$$

where a and b are normalizing constants and ΔF, ΔS, ΔN denote the changes in the total functioning value F, the species richness S and total abundance N between two communities A and B. $\overline{w_A}$, $\overline{\Delta p}$ and $\overline{F_A}$ refer to the arithmetic mean of the functioning weights of the species in A (the trait values), the mean change in relative trait abundance p and the average value of functioning in A. Therefore, this approach allows for a simple decomposition of richness, and compositional and abundance effects on ecosystem functioning. The quotient $\frac{\overline{w_A}\,\Delta S}{\Delta F}$ quantifies the relative impact of species richness on the change in functionality or ecosystem service. In a next analytical step, the decomposed differences in functioning between pairs of study sites might be related to respective differences in well-being leading to two dissimilarity matrices that can be linked by bi- or multivariate matrix regression. This approach appears to be particularly promising as it bypasses the functionality step in an elegant way.

3.6 | Structural equation modelling

Direct bivariate correlations are descriptive as they do not inform about causal relationships. Although structural equation modelling SEM (path analysis) is also based on linear correlations the complex model structure, including hidden (latent) variables, provides at least hypotheses about such causal dependencies (Kline, 2016; Shipley, 2016). Ideally, the relationships identified in Figure 3 form a basic path analytical network that can be simplified into models of latent and hidden variables dependent on data availability. Path analytical approaches are data hungry and only a few studies have used these models for inferences of ecosystem functioning (Mardani et al., 2017). The potential of this approach is still not fully realized. Traditionally, SEMs are used to infer human influences on diversity and ecosystem functioning (e.g. McKinney et al., 2010; Schweiger et al., 2016). Often the results can be interpreted as a negative relationship between diversity and human well-being. From a complex path model including direct and indirect biodiversity drivers of human well-being Santos-Martín et al. (2013) inferred positive effects of biodiversity on well-being mediated by regulating ecosystem services and negative effects when mediated by provisioning ecosystem services. These contrasting results exemplify the methodological and conceptional difficulties when linking diversity and human well-being. These difficulties are often downplayed in current conceptual reviews of the state of the art (e.g. Naeem et al., 2016).

In this respect, particularly partial least squares path analysis (PLS PM) with its bootstrapped-based extensions appeared as a promising tool in the field of ecology and human well-being despite the fact that it is mainly applied in social and chemical sciences, so far. Despite current discussion about the validity of the model (e.g. Rönkkö et al., 2016) PLS PM has proven to be an appropriate tool to explore the functioning of complex systems involving highly correlated predictors and missing data. It focuses on latent variables and avoids estimation biases from unequal and too low or too high sample sizes (Henseler et al., 2015; Kock, 2019; Tenenhaus et al., 2005).

3.7 | The multifunctionality pathway

The concept of ecosystem multifunctionality, the holistic view of the joint effects of different ecosystem functions, has important implications for the analysis of diversity–well-being relationships (Manning et al., 2018). Field work and simulation models have revealed that species diversity is positively linked to multifunctionality at different spatial scales (Allan et al., 2015; Hector & Bagchi, 2007; Meyer et al., 2018; Suárez-Castro et al., 2022; but see Birkhofer et al., 2018). However, this link is partly implicit due to the definition of multifunctionality as the ability to provide multiple functions. These multiple functions require diversity.

Meyer et al. (2018) highlighted how the way of quantifying multifunctionality determines the strength of this relationship. Different metrics (using sums of standardized functioning values or respective upper thresholds possibly in combination with case-specific weight functions) have different statistical properties (Byrnes et al., 2014). Unfortunately, no study so far has compared these metrics using standard benchmark tests. We feel that such a benchmarking is particularly necessary as the common ecological definition of multifunctionality is too imprecise to allow for unequivocal metric use and conclusions. In our view, it remains unclear whether observed multifunctionality–well-being relationships were merely the result of the choice of the metric–test statistics combination. An appropriate quantification of community or ecosystem multifunctionality might provide a direct link from underlying compositional diversity to the multifunctionality impact on well-being.

3.8 | The environmental pathway

Environmental conditions might directly influence human and animal well-being (FAO, 2021; MA, 2005). In many instances, biodiversity and ecosystem functions directly influence these environmental conditions, form example in agricultural soils (Wall et al., 2015). Therefore, and instead of looking at ecosystem services we might study the indirect impact of diversity on well-being using an environmental pathway. In this respect, the positive tripartite and quadripartite relationships between to soil diversity, fertility, and plant productivity (→ well-being) are well established (Delgado-Baquerizo et al., 2017). However, this and other indirect diversity–human health relationships consider agricultural landscapes only. (e.g. McGuinness & Dowling, 2009) In turn, in a recent metagenomic comparison between organic and conventional farming Hausmann et al. (2022) failed to find significant differences in insect, particularly pollinator diversity that might influence plant productivity and food quality. The question whether and in which natural ecosystems higher diversity positively influences those environmental characteristics that might affect human well-being still deserves much attention and is far from being settled. We call for an integrative framework that identifies candidate positive and negative quadripartite relationships across various natural and anthropogenic habitats.

4 | MEASUREMENT ISSUES

Diversity is quantified by species richness or some dimensionless ratio (e.g. Shannon index). Respectively, ecosystem functions and services are given either by ratios (stability or resilience ratios) or amounts with appropriate dimensions (e.g. monetary value or kg CO_2 absorption × m^{-2} leaf area). Evaluating these by regression-based models including ANOVA needs parameters that standardize dimensions to become comparable. Dimension analysis is a neglected aspect of ecological modelling as these are most often treated as simple normalization constants (e.g. Brown et al., 2004; Niklas & Hammond, 2019). However, in multivariate analysis with several parameters, parameter interpretation and also possible parameter dependences are an increasing issue.

This autocorrelation effect of parameters has been intensively discussed within the biological scaling literature (e.g. Glazier, 2010; Peters, 1983) and stems mainly from external constraints acting on the parameters (Glazier, 2010). In the ecological literature parameter autocorrelation of additive linear and nonlinear models has largely been ignored. Recently, Pillai and Gouhier (2019) have stimulated a discussion around non-independencies and parameters interpretation of the widely used Price partition (Fox, 2006; Loreau & Hector, 2001). Pillai and Gouhier (2019) and van Veelen (2020) argued that the widely accepted partitioning of changes in plant trait expression into richness and complementary effects cannot unequivocally be used to infer positive effects of species richness on ecosystem functioning due to parameter non-independence (but see Ulrich et al., 2022). This example highlights the possible problems in causal inference with respect to diversity effects on various other patterns and processes including human health. Similarly, the widely used partitioning of change in diversity, that is β-diversity, into effects of richness and community composition (Baselga, 2010; Podani & Schmera, 2011) does not necessarily result in fully independent partitions, again making unequivocal interpretation and causal inference challenging, particularly at small effect sizes of richness effects.

4.1 | Variability and well-being

Most studies on diversity, ecosystem functioning and well-being centre variable expressions averaged over focal habitats or landscapes. Our conceptual framework as shown in Figure 3 also relies on average parameter expressions. Recent theoretical (Loreau et al., 2021) and observational work (Allan et al., 2014; Gossner et al., 2016) however, drew attention to the importance of spatial and temporal habitat heterogeneity causing variability in species richness and ecosystem functioning and to increasing faunal and floral homogenization in intensively used agricultural landscapes. From basic aggregation and insurance models of variability (Sevenster, 1996; Yachi & Loreau, 1999) it is now well understood how temporal and spatial variability in abundances and community composition enhances stability of aggregate ecological variables like biomass, productivity, soil production, water retention or carbon sequestration (Wang et al., 2021).

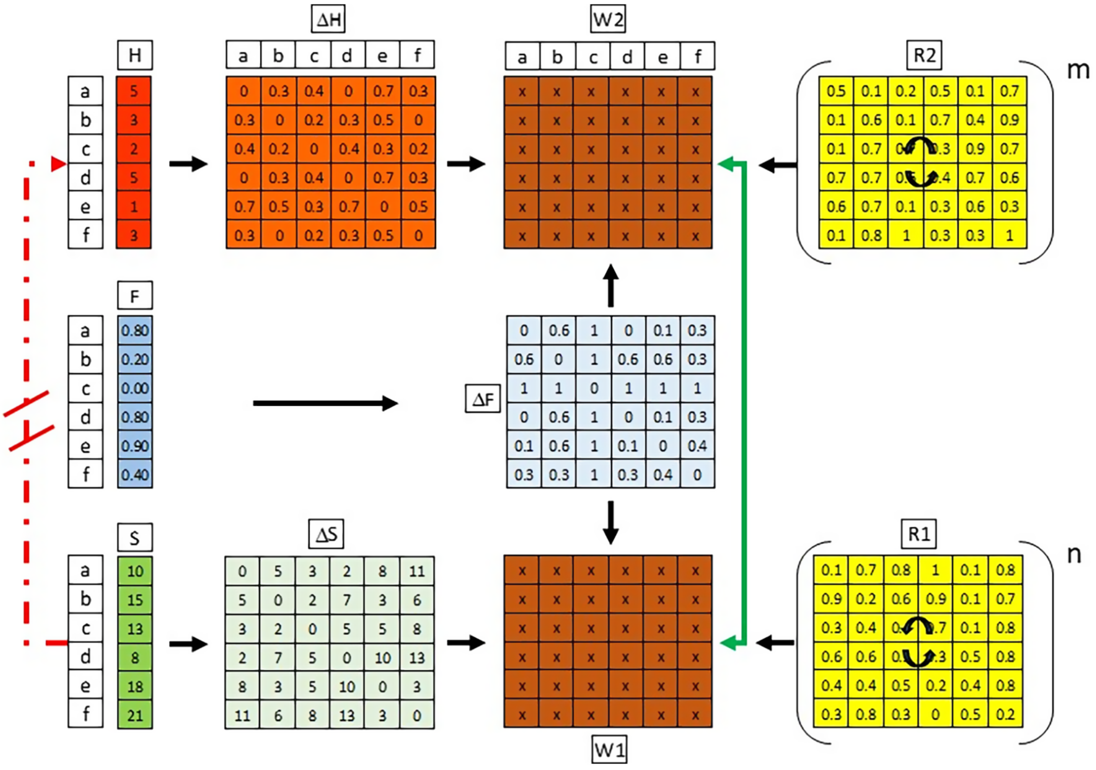
The principal question is now whether and how variability in community composition (compositional diversity), in functional diversity, and in the expression of ecosystem services influences focal aspects of well-being. This question has not received sufficient attention so far but is of major theoretical interest (Garibaldi et al., 2018). Do homogenous agricultural or otherwise managed landscapes with high levels of provisioning and non-provisioning ecosystem services contribute more to human well-being than more natural heterogeneous landscapes with lower levels of provisioning and non-provisioning ecosystem services? Quantification of the net benefits from these different landscapes would require data for ecosystem services and quantification of effects on well-being from a series of landscapes with different levels of diversity.

4.2 | Space–time discongruency

Any identification of the influence of ecosystem services on human well-being is confronted with the problem of space–time discongruency. By this we mean that studies on the influence of ecological diversity or functioning on aspects of human well-being are confronted by the time lags between changes in diversity and ecosystem functioning and visible well-being effects (Garibaldi et al., 2018). The time interval required for measurable effect sizes is often unknown and clearly case specific. For example, invasive species often show a considerable period of slow population increase until negative effects on ecosystem functioning become visible (Crooks & Soulé, 1999; Gentili et al., 2021). In this respect, threshold or tipping point effects need to be considered (e.g. Dakos et al., 2019). For instance, a decline in pollinator richness negatively influences pollination and consequently crop or fruit production (e.g. Stein et al., 2017). However, depending on crop or fruit type measurable effects might be visible only beyond some threshold level, while below the threshold functional responses in pollination might mask effectivity issues (e.g. Montoya-Pfeiffer et al., 2020). Felipe-Lucia et al. (2020) have demonstrated how landscape homogenization might change the trade-offs between diversity, ecosystem functioning, and ecosystems services at regional scales. Therefore, we need information on the spatial scale at which diversity–well-being relationships might be apparent.

4.3 | Direct versus indirect testing

Most work on diversity–well-being relationships uses evidence-based inference testing the hypothesis of positive diversity effects (cf. Marselle et al., 2021). This is done within the Pearson-Neyman or Bayesian frameworks. Both approaches need comparatively strong evidence, that is high effect sizes, for hypothesis acceptance. Importantly, well-being is a process spread in time, where small effects during a lifetime might accumulate to gain visible consequences at an older age. Irrespective of the statistical framework we would either need long-term studies or a high number of single studies or study sites within a single analysis to reach common significance thresholds. However, such comparisons raise concerns of data comparability and compatibility. As a consequence of statistical rigour many positive diversity–well-being relationships will remain undetected leaving us with the simplest and most obvious relationships. These few detectable relationships may, however, not be the most important with respect to biodiversity management.



H

	H
a	5
b	3
c	2
d	5
e	1
f	3

ΔH

a	b	c	d	e	f
0	0.3	0.4	0	0.7	0.3
0.3	0	0.2	0.3	0.5	0
0.4	0.2	0	0.4	0.3	0.2
0	0.3	0.4	0	0.7	0.3
0.7	0.5	0.3	0.7	0	0.5
0.3	0	0.2	0.3	0.5	0

W2

a	b	c	d	e	f
x	x	x	x	x	x
x	x	x	x	x	x
x	x	x	x	x	x
x	x	x	x	x	x
x	x	x	x	x	x
x	x	x	x	x	x

R2

0.5	0.1	0.2	0.5	0.1	0.7
0.1	0.6	0.1	0.7	0.4	0.9
0.1	0.7	[illegible]	0.3	0.9	0.7
0.7	0.7	[illegible]	0.4	0.7	0.6
0.6	0.7	0.1	0.3	0.6	0.3
0.1	0.8	1	0.3	0.3	1

F

	F
a	0.80
b	0.20
c	0.00
d	0.80
e	0.90
f	0.40

ΔF

0	0.6	1	0	0.1	0.3
0.6	0	1	0.6	0.6	0.3
1	1	0	1	1	1
0	0.6	1	0	0.1	0.3
0.1	0.6	1	0.1	0	0.4
0.3	0.3	1	0.3	0.4	0

S

	S
a	10
b	15
c	13
d	8
e	18
f	21

ΔS

0	5	3	2	8	11
5	0	2	7	3	6
3	2	0	5	5	8
2	7	5	0	10	13
8	3	5	10	0	3
11	6	8	13	3	0

W1

x	x	x	x	x	x
x	x	x	x	x	x
x	x	x	x	x	x
x	x	x	x	x	x
x	x	x	x	x	x
x	x	x	x	x	x

R1

0.1	0.7	0.8	1	0.1	0.8
0.9	0.2	0.6	0.9	0.1	0.7
0.3	0.4	[illegible]	0.7	0.1	0.8
0.6	0.6	[illegible]	0.3	0.5	0.8
0.4	0.4	0.5	0.2	0.4	0.8
0.3	0.8	0.3	0	0.5	0.2

FIGURE 5 Indirect inference using a manifold of random matrices (yellow) to infer most probable values of link functions (grey) between numbers of species *S* at *six* sites (a–f, green matrices), ecosystem functioning values *F* (blue), and well-being *H* (red). Direct inference from richness to well-being is often not possible (disrupted red arrow). Indirect inference uses a manifold of random 6×6 matrices (R1, R2, yellow). Multiplication of these matrices with the richness and well-being dissimilarity matrices Δ*S* and Δ*H* among sites provides estimates for the functioning dissimilarity matrix: $\Delta F = R1^n \times \Delta S$; $\Delta F = R2^m \times \Delta H$, tested for different values of *m*, $m \geq 1$. A subset of matrices W1 and W2 that best provide estimates for Δ*F* are then compared for similar structures of weight values (green arrow). In case of positive diversity–well-being relationships equivalent matrix values should correlate.

One way out of this dilemma would of course be the change of perspective. It is obvious that without wildlife humans would no longer exist. Therefore, the natural null hypothesis is that diversity begets well-being and contestants need to demonstrate the contrary. A more feasible solution might be based on indirect inference models as used in econometrics (Gouriéroux et al., 1993). Indirect inference models are applied in cases where datasets are too large or where data are partly unsuited. They use a manifold of simulated relationships to estimate the most probable parameter combinations (Jiang & Turnbull, 2004). In community ecology, respective so-called reverse engineering models have been developed to estimate the most probable coefficients of competitive strength in multispecies communities, where the degrees of freedom are too high for direct analytical solutions (Ulrich et al., 2014). Empirical Bayes approaches that estimate Bayesian priors from empirical data can also be seen from the indirect perspective and have been applied to the assessment of non-random species associations (Casella, 1985; Gotelli & Ulrich, 2010).

With respect to diversity well-being relationships, we are confronted with the problem that the weight functions in Figure 3 that link diversities to ecosystem functioning values and subsequently functioning to well-being are generally not known. The limited numbers of sites in most studies do not allow for a direct analytical assessment. Therefore, we might use diversity, functioning, and well-being dissimilarity matrices obtained from a number of study sites and compare two randomly constructed matrices of weight values obtained from the linear and nonlinear fitting of richness and well-being to functioning (Figure 5). This fitting with random matrices is repeated until a stable peak in goodness of fit is reached and might include calculations of thousands of matrices depending on the numbers of sites to be compared. If diversity and well-being were related, we should find some joint structures in the best fitting weight matrices. Importantly, these weight matrices might serve as priors in Bayesian analysis to apply to different sets of study sites.

RECOMMENDATIONS

This methodological review has to be seen as a cautionary note. Although positive direct and indirect influences of biodiversity on human well-being are most likely, unequivocal evidence is still scarce and restricted to cases like pollination—crop and honey production. These case studies are still important, but we call for a stricter terminology for the different aspects of functioning, multifunctionality and well-being (Figure 1) and highlight the need to evaluate each step in the pathways from diversity to well-being (Figure 3). More analyses should be based on matrix and path analytical techniques, and on functioning partitions including potential covariates rather than on bivariate comparisons. We call for appropriate long-term socio-ecological research platforms to gather relevant data about ecosystem functioning and well-being across space and time. We also highlight the need to consider potential trade-offs in diversity effects and to include ecosystem disservices for a full understanding of the ecological constraints on human well-being.

AUTHOR CONTRIBUTIONS

Werner Ulrich conceived the idea, developed the figures and wrote the first draft. Adrien Rusch, Péter Batáry, Klaus Birkhofer, and Enrique G. de la Riva gave major conceptual and literature input. All authors contributed to the development of the conceptual figures and the final text version.

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CONFLICT OF INTEREST

We declare no conflict of interests.

DATA AVAILABILITY STATEMENT

No data are linked to this publication.

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