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REVIEW

A network prediction model to quantify relationship between biodiversity and ecosystem functioning (BEF)

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Abstract

1. Biodiversity loss has a large impact on many ecosystem functions (EFs). It is urgent to quantify the effect of biodiversity loss on EFs, and much efforts are needed to determine quantitatively the relationship between biodiversity and ecosystem functions (BEF).
2. In this review, we first summarised the mechanistic models commonly applied in current BEF studies, and proposed a new BEF model based on species interaction networks. The 'network attenuation model', which is built up by an unsaturated network, quantifies BEF. Then, the implication of network attenuation model for the scale dependence of BEF has been studied. Finally, the network attenuation model has been tested using data from the BIODDEPTH project.
3. We found that fitting models with the network attenuation model provided better results than other common fitting methods. The model fitting results revealed the scale dependence in BEF relationships, and demonstrated nonlinear changes in the BEF-slope with the spatial scale.
4. We conclude that the network attenuation model can be used as an alternative approach to estimate BEF, and the information from this model can provide meaningful guidance for the allocation of resources for conservation efforts worldwide. More efforts will be necessary assess the effect of biodiversity on various EFs as the importance of interactions among species and species richness may also vary over time.

KEYWORDS

biodiversity, ecosystem function, network analysis, species interaction network

1 | INTRODUCTION

Loss of biodiversity has an impact on ecosystem functioning worldwide, but we lack an in-depth understanding of how this loss may influence ecosystem functions (EFs), such as primary productivity or soil and water processes, in the long term (Ramus et al., 2022). Many studies investigating the relationship between biodiversity

and ecosystem functioning (BEF) have focused on the level at which biodiversity loss is critical to maintain a certain level of EF (Furey & Tilman, 2021; van der Plas, 2019). For example, it has been demonstrated that, in order to maintain EFs such as carbon sequestration or soil functioning to a high level of performance, species decline within an ecosystem must not exceed 20% (Newbold et al., 2016). If this critical threshold is exceeded, manual interventions are required

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to sustain an efficient EF level. However, how does biodiversity directly or indirectly affect EF? How species interact and how these interactions contribute to maintain EF? To further clarify these questions, it is necessary to quantify the effect of biodiversity on different EFs while decreasing the uncertainty of effects of biodiversity loss on EFs (Oliver, 2016).

The quantification of the correlation between biodiversity and EF has a long history, with the establishment of various correlation models. Generally, studies support a positive correlation between biodiversity and EF (Cappelli et al., 2022; Daam et al., 2019), and model evaluations indicate that log-linear, linear and other type of relationships accounted for 53%, 39% and 8% of biodiversity-EF correlations, respectively (Srivastava & Vellend, 2005). Other studies have also suggested that the BEF can be expressed using the Michaelis–Menten equation (Cardinale et al., 2012):

$$EF = EF_{\max} \left(\frac{K}{S + K} \right), \quad (1)$$

where S refers to the biodiversity measure and K refers to the value of S when $EF = \frac{1}{2} EF_{\max}$, which is the max value of EF . Due to differences among climate, soil types and vegetation, the Michaelis–Menten equation is not universal for all ecosystems (Mora et al., 2014). In order to take into account environmental impacts, BEF simulations have been performed based on natural gradients or along gradients of environmental stress. For example, Baert et al. (2018) proposed a BEF unimodal relationship that is dependent on environmental stress variations, with the effects of biodiversity on EFs being maximised at medium levels of environmental stress.

These correlation models make a great effort in clarifying BEF. For instance, Gheysari et al. (2015) showed that most relationships between bacterial diversity and EFs were exponential and/or linear, which suggests that a loss of even a small number of bacterial species can have a strong negative impact on overall ecosystem functioning. However, statistical models do not allow to assess the mechanisms behind BEF, especially because the direct or indirect effects of biodiversity on EF are not well identified and understood (Newbold et al., 2016). So, much effort is still needed to determine quantitatively EF. To better clarify this issue, we first summarised the mechanistic models currently applied in most BEF researches, and then proposed a new BEF model, the ‘network attenuation model’, which was named based on network analysis and the curve shape of the model. We then tested this model using data from natural ecosystem and compared it to most of classical approaches.

2 | MECHANISM AND QUANTIFICATION OF BEF

Several researches have shown that the effects of biodiversity on EF may consist of many different factors (Daam et al., 2019; Huang et al., 2022; Mora et al., 2014). Loreau and Hector (2001) divided these effects into two groups: complementarity effect and selection effect. The former arises from niche differentiation or facilitation

between species whereas the latter effect arises from natural selection, such as interspecific competition, which can favour dominant species with particular functional traits within a community (Yang et al., 2022). Moreover, a community with higher plant species diversity can have a higher chance of containing a dominant species, and thus can achieve a higher EF (Loreau, 2001). However, it is not clear whether the functional consequences of biodiversity come from niche complementarity or selection effect?

Based on a large subtropical forest BEF experiment in China, Huang et al. (2022) analysed the relationship between biodiversity and plant biomass. The results showed that tree species diversity may promote productivity mainly by niche complementarity. Similarly, Erickson et al. (2015) showed that niche complementarity increased in communities with a higher species richness. The results from these researches highlight that the relationship between biomass and niche complementarity is more likely than that with the selection effect. In another study carried out by Hodapp et al. (2016), the authors emphasised that both niche complementarity effect and selection effect depended on environmental heterogeneity (e.g. soil properties), with an increasing niche complementarity as heterogeneity increases in the environment. In addition, Cadotte (2017) demonstrated that selection effect was the main factor in explaining diversity effects in a community characterised by a high species richness and a low diversity of functional traits, while niche complementarity was the main factor explaining biodiversity effects in a community with a high diversity of functional traits. These results suggest that niche complementarity and selection effect can be explained by species functional traits, with selection effect playing only a minor role in explaining EFs. For example, if selection effect determines EF, a dominant species with a particular fitness trait is supposed to be the main driver of the EF. But other species can also have this fitness trait and contribute to explain EF. In comparison, niche complementarity effect depends strongly on species composition (Cadotte, 2017). Although this theoretical framework has considerably improved our understanding of BEF, studies in the literature have not reached a consensus yet.

Based on a theoretical analysis of BEF, Loreau (1998) proposed a model research that is considered as the most influential work for current studies that quantify the impact of biodiversity on EF. In this model, the four parameters ($DT, D_i, \bar{D}, D_{\max}$) used to quantify the effects of diversity on EFs are first defined. M_i and O_i refer to the yield of species i under individual and mixed cultivation conditions in a cultivation test, respectively, and p_i and E_i denote the plant proportion and expected yield of species i under mixed cultivation conditions, respectively. Then E_i can be expressed as

$$E_i = M_i \times p_i, \quad (2)$$

and the overall yield variation induced by species interactions (D_T) can be calculated as

$$D_T = \frac{\sum O_i - \sum E_i}{\sum E_i}. \quad (3)$$

Moreover, under mixed conditions, the yield variation of species i induced by other species (D_i) can be calculated as

$$D_i = \frac{O_i - E_i}{E_i}. \quad (4)$$

In the sample area, the average yield variation of different species induced by species interactions (\bar{D}) can be calculated as

$$\bar{D} = \sum p_i D_i. \quad (5)$$

These equations regard species interactions as the effects of biodiversity and yield (Loreau & Hector, 2001):

$$\Delta Y_j = N_j \cdot \overline{\Delta RY_{ij}} \cdot \bar{M}_i + N_j \cdot \text{cov}(\Delta RY_{ij}, M_i), \quad (6)$$

where ΔY_j refers to the net effect of biodiversity on biomass in mixed sample area j , $\overline{\Delta RY_{ij}}$ refers to the arithmetic mean of ΔRY_{ij} of all species in mixed sample area j ; ΔRY_{ij} refers to the difference between the practical and expected relative yields of species i in mixed sample area j , N_j refers to the quantity of the species in mixed sample area j , and \bar{M}_i refers to the average biomass of species i under individual cultivation conditions. More specifically, ΔY_j is defined as the difference between observed and expected biomass for all species in mixed sample area j . The expected biomass of a species in mixed sample area j is expressed as the product of the plant proportion of the species in mixed sample area j and its biomass under individual cultivation conditions (M_i). The first term on the right-hand side of the equation refers to the biomass change caused by the niche complementarity effect and

$$\Delta RY_{ij} = \frac{Y_{ij}}{M_i} - p_{ij}, \quad (7)$$

where Y_{ij} refers to the observed biomass of species i in mixed sample area j , and p_{ij} refers to the proportion of species i in sample area j . The second term on the right-hand side of the equation refers to the biomass variation in the sample area caused by natural selection. Furthermore, $\text{cov}(\Delta RY_{ij}, M_i)$ refers to the covariance of ΔRY_{ij} and M_i for all species in sample area j . The equation adopts the probability theory identity where by the weighted average is equal to the arithmetic mean plus covariance. In addition, $N_j \Delta RY_{ij}$ is equal to \bar{D} (Loreau, 1998) and can be expressed as the niche complementarity effect. If biomass M_i is taken as a variable, then ΔRY_{ij} is the species weight, and the covariance is employed to measure the consistency between these two variables. Variations in species weights can refer to the survival of species induced by natural selection in the sample area. Specifically, the survival can be quantified using the covariance of the weight and initial biomass. Species weights with a positive covariance and high yield exhibit an increase in value, while species weights with a negative covariance and low yield exhibit a decrease in value.

However, some scholars disagree with the work of Loreau (1998). For example, Pillai and Gouhier (2019) claim that the division of the net biodiversity effect into selection and complementarity effects is inappropriate, as it is based on a low-level hypothesis, and cannot explain the non-linear correlation between species abundance and

EF. Because non-linear relationships is common in nature, this may lead to the over-estimation of the net effect of biodiversity (Pillai & Gouhier, 2019).

To further understand the underlying mechanisms, numerous models have been proposed recently. For example, Lefcheck et al. (2021) applied a decomposition approach inspired by the 'Price equation', which is a tool that quantifies how trait frequency changes over time as a result of natural selection and gene transmission, to a global dataset of reef fish community biomass. The results indicated that species identity and richness both contribute to BEF. Furthermore, Brophy et al. (2017) applied diversity-interactions models in order to simulate the effects of species richness, species evenness, species interactions and specific species effects on EFs. This study demonstrated that the effects of the multiple facets of diversity described above can be effectively evaluated based on diversity-interactions models. Therefore, there is an increasing necessity to develop new quantification methods that assess EFs based on species interaction networks in order to better understand and evaluate BEF relationships.

3 | FROM BIODIVERSITY TO SPECIES INTERACTION NETWORK

Species interactions can be a much better indicator of EF than a simple list of taxa and related biodiversity indicator variables (Chang et al., 2022; Valiente-Banuet et al., 2015). Recently, the number of publications proposing new estimators of species richness and diversity has considerably increased, and new and innovative approaches such as remote sensing technology have been proposed to obtain such estimates (Chao et al., 2019; Skidmore et al., 2021; Williams et al., 2021). Yet, sampling species or taxa-specific biodiversity variable represent only a single component of biodiversity, and interactions among species are another fundamental component of biodiversity, which supports the existence, but in some cases also the extinction of species (Jordano, 2016). For example, the loss of interactions among species often represents a dramatic decrease in EFs (Valiente-Banuet et al., 2015). The loss of ecological interactions is often accompanied, or even preceded, by species disappearance (Jordano, 2016). Interactions among species are thus a key component of biodiversity, and biodiversity itself is the result of complex biotic interactions that are structured in species networks. In some case, it has also been found that EFs can change with changing the species interaction network (Nie et al., 2023), and this without any change in the species richness (Morrien et al., 2017). This result emphasises that assessing species interactions should be central when identifying and quantifying EFs (Poisot et al., 2013).

Species interaction networks, in which species are represented as nodes and interactions as links, can be used as tools to examine how changes in biodiversity can affect species interactions and BEF (Morrison & Dirzo, 2020). The observed networks vary in properties such as the number of individuals in the network, the proportion of possible relationships that occurs, and the average frequency of

interactions (Ushio et al., 2022). Networks form the structural backbone of communities and can be parsed into two components: the topological network structure and the ecological network structure. Topological structure deals with the mathematical quantification of the network (i.e. how many species there are and how interactions are distributed among them), while ecological structure focuses on the identities of species and interaction partners within the network. Both components reveal complementary insights into the processes structuring networks and the response of networks to environmental disturbance (CaraDonna et al., 2017; Delmas et al., 2019).

Different topological network structure have been found in 'antagonistic' or 'mutualistic' networks (Morrison & Dirzo, 2020). Antagonistic networks are typically modular. It means that species are tightly linked with fewer interactions across modules (Cagnolo et al., 2011). Modularity in antagonistic networks can arise from evolutionary constraints on interactions (Lewinsohn et al., 2006). For example, the co-evolutionary 'arms race' between herbivores and plant hosts can result in greater reciprocal specialisation between partners (Cagnolo et al., 2011). Mutualistic networks tend towards a nested structure that implies interaction asymmetry, and species with few interaction partners interact with subsets of species in this structure (Bascompte et al., 2003).

4 | NETWORK ATTENUATION MODEL: A NEW PREDICTION MODEL FOR BEF

In general, species interactions can be illustrated with bipartite graphs, with two or more distinct groups of interacting partners (Bascompte & Jordano, 2007). The matrix entries illustrate the values of the pairwise interactions visualised in the Δ matrix, and can be 0 or 1, for presence-absence of a given pairwise interaction, or take a quantitative weight w_{ji} to represent the interaction intensity or unidirectional effect of species j on species i (Bascompte & Jordano, 2007). If the unidirectional effect is neglected, and the value of pairwise interactions between every two species of an ecosystem is equal, the relationship between the number of species interactions (SI) and species richness (n) can be expressed as:

$$SI_0 = 0.5n^2 - 0.5n, \quad (8)$$

However, in real-world, SI cannot increase unlimitedly with n . The reason is due to the forbidden links, which are defined as non-occurrences of pairwise interactions that can be accounted for by biological constraints (Jordano, 2016). In other words, independently of whether we sample full communities or subset communities, some of the interactions found in the empty adjacency matrix Δ do not occur in natural conditions (Jordano, 2016). Forbidden links are thus represented as structural zeroes in the interaction matrix. Although we still have very little information about the frequency of forbidden links in natural communities (Maruyama et al., 2014; Valiente-Banuet et al., 2015), what we do know is that forbidden links can

slow SI to a maximum in a natural community as n increases, because of the attribution of forbidden links. In order to integrate this information into the relationship between SI and n , we used the form of the following equation:

$$y = y_{\max} \left(1 - \frac{1}{\frac{x}{Q} + 1} \right), \quad (9)$$

where y is the dependent variable and x is the independent variable. y is going to get closer to the maximum y_{\max} with the increase of x , and the speed depends on the parameter Q . In this formula, y cannot increase indefinitely as x increases because it is constrained by y_{\max} and Q . We replace y with SI , replace x with $0.5n^2 - 0.5n$, and then merge the Equations (9) and (10) as follow:

$$SI = SI_{\max} \left(1 - \frac{1}{\frac{n^2 - n}{2Q} + 1} \right), \quad (10)$$

where SI_{\max} is the maximum of SI in an ecosystem, Q is a parameter related to forbidden links, and the value of Q can determine the shape of SI with increasing species richness. According to the above discussion, species interactions are at the core of ecosystem functions (EFs). More specifically, a given EF can be expressed by a given species interaction (SI) within an ecosystem. In this context, everything can be expressed as an interaction. For example, seeds are the results of sexual interaction. Seed germination and seedling growth are the results of the interaction between organisms and environmental factors such as soil, air and water. For an ecosystem, net primary productivity (NPP), an important EF, is first determined by the interaction between species within the community and abiotic environment. Second, species diversity can also affect NPP through niche complementarity, the facilitation between species, and interspecific competition. Such mechanisms can be thought of as interspecies interactions. Thus, in a relatively stable abiotic environment, changes in NPP are primarily influenced by species interactions. A relatively stable abiotic environment denotes a limited spatial variability and strong temporal stability of the environment factors. In such an environment, NPP can be expressed as a variable component resulting from the interaction of species and a constant component resulting from the interaction of species with abiotic environmental factors:

$$EF = \alpha SI + EF_0. \quad (11)$$

α is a coefficient related to the dimension of EF which is NPP in this example. EF_0 is a constant, which is the initial value of EF for a given ecosystem, and the value of EF_0 is related to the interaction between species and their abiotic environment in the ecosystem. Then, Equations (10) and (11) can be merged, and a new prediction model for predicting EF can be achieved as follows:

$$EF = (EF_{\max} - EF_0) \left(1 - \frac{1}{\frac{n^2 - n}{2Q} + 1} \right) + EF_0, \quad (12)$$

with EF_{\max} being the maximum of a EF in a given ecosystem. Figure 1 describes the curve form of formula (12). In addition to NPP, we suggest

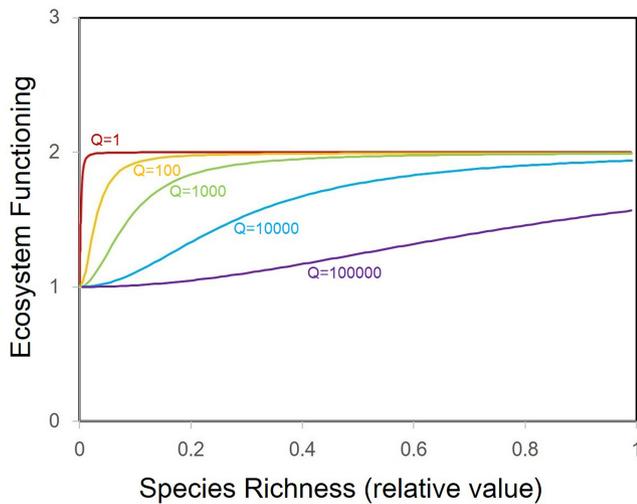


FIGURE 1 The curve of network attenuation model.

that other types of EF, such as soil and water processes, can also be estimated through species interactions based on this method. In particular, a given EF can be expressed by a given *SI* within an ecosystem, and different EFs can be expressed by different *SIs* within a given ecosystem. Although further experiments are required to prove this hypothesis, we initially built the model based on it and subsequently tested the predictive applicability of the model. While it is unclear which relationships and species should be considered to express a given EF (e.g. NPP or soil and water processes) in the proposed model, we can achieve the optimal fitting of a given EF and species richness within an ecosystem by correcting the parameter *Q* according to actual data.

In summary, based on the hypothesis that a given EF can be expressed by a given *SI* within an ecosystem, a network attenuation model was built to fit the relationship between the EF and species richness. The shape of the fitted curve is principally affected by forbidden links among species, which can be measured by the parameter *Q*. So, the model can indirectly quantify the effects of biodiversity on ecosystem function by measuring the intensity of interactions between species. Overall, a positive relationship is observed between the value of *Q* and the number of forbidden links in an ecosystem. For example, when the value of species richness is fixed, the number of forbidden links gradually increases with *Q*, *SI* decreases, and EF decreases accordingly (Figure 1). Thus, for a small actual sampling gradient of the species richness, the slope of the BEF is likely to decrease as *Q* increases. The larger the *Q* value, the flatter the BEF relationship curve.

5 | ASSUMPTIONS/PRECONDITIONS FOR USING NETWORK ATTENUATION MODEL

From the description above, we stipulated three assumptions/preconditions regarding the network attenuation model. *Assumption 1*: Compared with inter-species interactions, intra-species interactions had negligible effects on EF, and the measurement of BEF can be simply transferred to the quantification of the relationship between

species richness and inter-species interaction. We acknowledge, however, the necessity to assess the role of intra-specific diversity in future assessment of interaction networks, notably because intra-specific diversity can explain up to 25% of overall community variation in some cases (Fridley & Grime, 2010). Thus, it will be necessary to incorporate this information into the network attenuation model in an improved version; *Assumption 2*: Network attenuation model is established to simulate natural phenomena in its original version. Because human activity can affect directly EFs in managed ecosystem (Yu et al., 2023), the model in its current version is not recommended for disturbed areas; *Assumption 3*: Within a space and time scale of BEF research, abiotic environmental conditions are relatively homogeneous, and the interaction between an organisms and its environment is considered as relatively constant. It is important to note that this assumption is not an absolute requirement. It means that this model is more effective under the condition of relatively homogeneous environment at small spatiotemporal scales than heterogeneous environments at relatively large spatiotemporal scales. The relevant theory involves the scale dependence of BEF, and the derivative process can be shown in the next section.

Under these three hypotheses, increasing species richness will increase EF until a plateau (Figure 1). However, it is important to note that different types of curve for the relationship between species richness and EF, such as humped back or exponential relationships, can also be found in some cases (Albrecht et al., 2021; Luo et al., 2022), especially in scenarios that do not follow the *assumptions* described above. For example, in order to keep a relatively homogeneous and constant abiotic environmental conditions, *Assumption 3* limits the scope of space and time of our model. But, if the conditions of space limitation are not met, spatial heterogeneity of the environment becomes more important to quantify BEF (Lefcheck et al., 2021; Wu et al., 2022). Furthermore, because BEF can vary across various ecosystems (Albrecht et al., 2021; Hu et al., 2021; Schiettekatte et al., 2022), the conclusions may differ in a heterogeneous environment. For example, it can be hard to quantify BEF within a landscape containing both forest and grassland (Figure 2). On the other hand, if the conditions of time limitation are not met, temporal stability of the environment can be disrupted, and the abiotic environment can markedly change with time. Because EF can be defined by the interactions between organisms and their abiotic environment, it is particularly difficult to quantify BEF in a changing environment. Therefore, it is reasonable to assume that different types of curve can be found over seasons and across years.

Moreover, it is important to note two limitations of the network attenuation model, which are important to consider when interpreting the results. First, one of the fundamental challenges of complexity is that most systems can be viewed in a variety of different, but equally correct, ways (Cumming, 2016). For example, ecological communities can be described by their populations of species, the nutrients that they contain, their processes or by their trophic interactions. Choosing one of these analytical lenses involves making choices about the scale(s) and level(s) of analysis, as well as the

phenomena of interests. Because differences in EFs come from different species interaction structure, there are different relationships between EFs and species richness, even within the same ecosystem. So, in principle, the network attenuation model represents the measure between one EF of interest and species richness at one given point in time.

Second, it is important to note that in practice, most surveyed networks to date have been subsets of much larger networks (Jordano, 2016). This is also true for protein interaction, gene regulation and metabolic networks, where only a subset of the molecular entities in a cell are targeted (Stumpf et al., 2005). Despite recent attempts to document 'whole ecosystem meta-networks' (Pocock et al., 2012), it is likely that most ecological interaction networks illustrate only a portion of all ecosystem compartments (Jordano, 2016). Due to their high temporal and spatial turnover as well as high complexity of association patterns, getting a complete overview of ecological interactions is challenging and requires large sampling effort. Therefore, to build a reliable relationship between species richness and EF with the network attenuation model, we can only rely on our underlying assumptions about ecosystem structure and take into account species that have a great effect on EF.

In conclusion, perfectly accurate relationship between species richness and EF, measured by network attenuation model, would be unrealistic. But, it is possible to make a nearly accurate relationship.

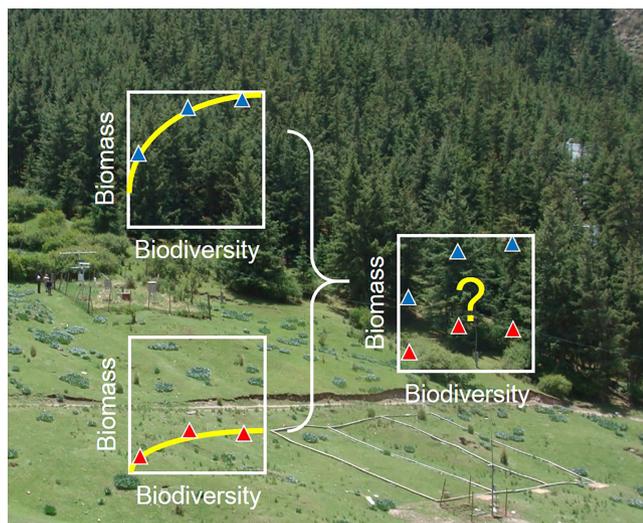


FIGURE 2 Quantification of relationship between biodiversity and ecosystem functioning in a composite landscape.

TABLE 1 The changing trends of parameters in network attenuation model with increasing of spatial scale for different scenarios.

	Scale	Q	EF_0	EF_{\max}	BEF-slope
Scenario 1	↗	↗*	Drastic changes are less likely	Drastic changes are less likely	↘*
Scenario 2	↗	↗*	Drastic changes are more likely	Drastic changes are more likely	↘

Note: Scenario 1 is an ideal conditions for model operation. In this scenario the heterogeneity of environmental factors is little considered. Scenario 2 is likely to meet in practice. In this scenario, the heterogeneity of environmental factors is considered. The direction of the arrow indicates the changing trends of model parameters with scale. An asterisk indicates a significant trend.

6 | EVALUATING THE BEF SCALE DEPENDENCE BASED ON THE NETWORK ATTENUATION MODEL

The scale dependence in BEF relationships has been reported in numerous studies (Keitt & Fischer, 2006; Sullivan et al., 2017). From the point of view of interaction, the BEF scale dependence can be described under two scenarios. Scenario 1 assumes that the environmental factors are almost homogeneous and do not vary with scale, representing an ideal state. In scenario 2, the heterogeneity of environmental factors is considered, which is more likely to occur in practice. In the following, we will analyse the changes in the network attenuation model parameters and BEF-slope under different scenarios.

In scenario 1, the variable EF_0 in the network attenuation model is related to the interaction between species and their abiotic environment when the environmental factors are almost homogeneous. Therefore, EF_0 is only affected by the variation of species as the scale changes. In contrast, EF_0 under scenario 2 can be affected by both the species and environment variation. Consequently, variations in EF_0 are more gentle in scenario 1 than scenario 2 under a changing scale. In addition, the species population size is limited and cannot increase indefinitely with the scale. Thus, as the scale increases, different species are more likely to become more spaced apart, and species interactions will become weaker. This is attributed to an increasing energy requirement for the movement of species. Based on this, in scenario 1, the forbidden links among species increase with the scale, and the value of Q in the network attenuation model is enhanced accordingly due its positive relationship with the former.

Unlike scenario 1, because of the strong influence of environmental heterogeneity on species, EF_0 (or the interaction between environmental factors and species) is likely to vary irregularly with the changing scale in scenario 2. Therefore, as the scale increases, EF_0 may be affected by both species and environmental variation, resulting in a greater magnitude of change in scenario 2 compared to scenario 1. However, similar to scenario 1, the forbidden links among species and the value of Q are also likely to increase with the scale in scenario 2.

In summary, parameter Q in the network attenuation model is likely to increase with the scale in both scenarios 1 and 2. However, the change in magnitude of EF_0 in scenario 2 may exceed that of scenario 1. As EF_{\max} can be defined as the sum of EF_0 and αSI_{\max} (Formula 11), the change in magnitude of EF_{\max} in scenario 2 can also exceed that of scenario 1. As a consequence, based on the network attenuation

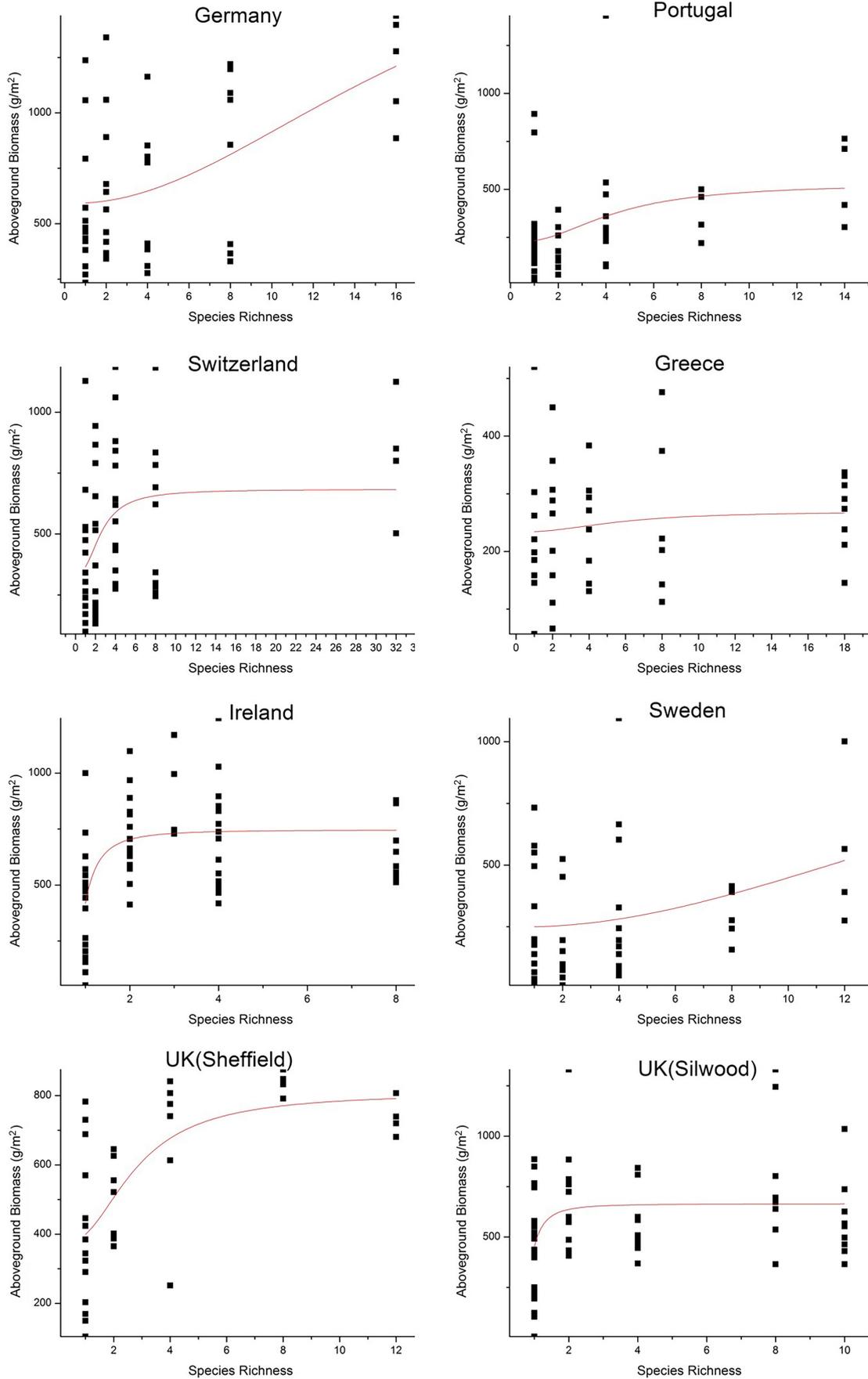


FIGURE 3 Fitting the relationship between species richness and above-ground biomass by network attenuation model, with the data from BIODEPTH.

	Network attenuation model	Linear model	Logarithmic model	Michaelis–Menten equation
Germany	0.2859	0.2826	0.2262	0.2466
Portugal	0.127	0.1206	0.1169	0.1228
Switzerland	0.1475	0.1118	0.1537	0.1493
Greece	0.014	0.0135	0.0152	0.0152
Ireland	0.3103	0.0698	0.1665	0.1444
Sweden	0.1	0.094	0.0669	0.0762
UK (Sheffield)	0.4613	0.3526	0.4414	0.426
UK (Silwood)	0.1286	0.0525	0.0823	0.0779
R^2 average value	0.196825	0.137175	0.1586375	0.1573

TABLE 2 The fitting results (R^2) for BIODEPTH by using network attenuation model, linear model, logarithmic model, and Michaelis–Menten equation.

model and from the perspective of interactions, as the spatial scale increases, it is more likely to observe a marked decrease in the positive BEF-slope in an almost perfectly homogeneous environment (scenario 1) compared to a heterogeneous environment (scenario 2). This is attributed to the more significant variation of parameters EF_0 and EF_{\max} under scenario 2 than scenario 1 (Figure 1; Table 1).

We can determine two key conclusions following the above analysis. First, for the case of a limited species richness sampling gradient, we are more likely to observe a decrease in the positive BEF-slope as the spatial scale increases. Second, the lower the environmental heterogeneity, the more significant the positive BEF relationship is with increasing the scale. In particular, a low spatial heterogeneity of an environment often corresponds to a smaller spatial scale, and thus the BEF is more likely to exhibit a significant positive relationship compared to larger scale environments. More specifically, species richness can have a great impact on EF at a small scale, yet at a larger scale, environmental factors are more likely to influence EF. Previous literature has supported this conclusion. For example, by analysing the species turnover in space and time, Gonzalez et al. (2020) demonstrated nonlinear changes in the BEF-slope with the spatial scale. Furthermore, Chisholm et al. (2013) performed a study on the relationship between species richness and forest productivity under a spatial extent ranging from 8 to 50 ha and revealed that the relationship between species richness and productivity changed with scale. The authors found a more significant positive relationship between species richness and productivity at the smaller scale, while environmental factors explained the variation in productivity at the larger scale (Chisholm et al., 2013).

7 | A MODEL APPLICATION EXAMPLE BASED ON BIODEPTH DATA

The BIODEPTH project contains 15 ecosystem-process variables measured at eight different European grassland field sites over 3 years (Hector et al., 2010). By using the data from this project, we evidenced that the network attenuation model is a robust fitting method when estimating the relationship between species

richness and EF, and can provide a better estimation than linear models, logarithmic models or the Michaelis–Menten equation (Figure 3; Table 2).

In general, the change in the fitting quality of network attenuation model for these eight field sites is similar with the other three models. For example, the fitting results for the field site in Greece by these four models have shown generally poor fitting quality (R^2 is from 0.0135 to 0.0152) (Table 2), whereas, the fitting results for the field site in UK (Sheffield) have shown commonly good fitting quality (R^2 is from 0.3526 to 0.4613) (Table 2). It is suggested that, similar to other models, the fitting quality of network attenuation model can be greatly affected by environmental heterogeneity. However, because there is an inflection point in the curve of network attenuation model, it can provide a better estimation of BEF in some case, such as in the field site of Ireland (Figure 3).

8 | CONCLUSIONS

In this work, we proposed to use the network attenuation model as an alternative method to estimate BEF. This model can indirectly quantify the effects of biodiversity on EF by measuring the intensity of interactions between species. By using this model under some conditions (see Assumption 1–3 in Section 5), we demonstrated that the network attenuation model was a better fitting method for BEF than many other common methods. This result highlights that interactions among species are effective to assess BEF. We conclude that the information from network attenuation models can provide meaningful guidance for conservation efforts worldwide, and more efforts will be necessary to assess the effect of biodiversity on various EFs as the importance of interactions among species and species richness may also vary over time.

AUTHOR CONTRIBUTIONS

Jian Hou and Nicolas Fanin conceived the ideas and designed methodology. Jian Hou and Zizhao Ni collected and analysed the data. Jian Hou led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflicts of interest to declare.

DATA AVAILABILITY STATEMENT

The data used in this study can be obtained from the websites: <https://www.science.org/doi/full/10.1126/science.286.5442.1123> and <https://doi.org/10.6084/m9.figshare.c.3303102>.

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