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PERSPECTIVE

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A quantitative framework for identifying the role of individual species in Nature's Contributions to People

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Abstract

It is widely acknowledged that biodiversity change is affecting human well-being by altering the supply of Nature's Contributions to People (NCP). Nevertheless, the role of individual species in this relationship remains obscure. In this article, we present a framework that combines the cascade model from ecosystem services research with network theory from community ecology. This allows us to quantitatively link NCP demanded by people to the networks of interacting species that underpin them. We show that this "network cascade" framework can reveal the number, identity and importance of the individual species that drive NCP and of the environmental conditions that support them. This information is highly valuable in demonstrating the importance of biodiversity in supporting human well-being and can help inform the management of biodiversity in social-ecological systems.

KEYWORDS
biodiversity, cascade model, community ecology, ecological networks, ecosystem functioning, ecosystem services, human well-being, social-ecological system, species identity

INTRODUCTION

Global biodiversity change has prompted widespread research into the relationship between biodiversity and Nature's Contributions to People (NCP) (IPBES, 2019), that is, the contributions, positive or negative, of the natural world to human quality of life. However, there have been few attempts to integrate this concept with established ecological theory (e.g., Felipe-Lucia et al., 2022; Keyes et al., 2021). This lack of theoretical integration limits the potential for ecological research to inform this major science–policy interface (IPBES, 2019). In this paper, we address this gap with a conceptual framework that integrates the cascade model of ecosystem services (Potschin & Haines-Young, 2011) with ecological network theory (Bascompte & Jordano, 2007). The resulting "network cascade" framework allows us to identify the role of individual species in the supply of NCP, alongside their importance, and the environmental conditions that support them.

Prior to the formulation of the NCP concept, the link between biodiversity and ecosystem functioning (BEF) has been thoroughly investigated in both experimental and observational studies. These studies typically relate measures of overall biodiversity (e.g. species or functional richness) to measures of ecosystem processes and properties, and typically find positive associations between biodiversity and rates of ecosystem functioning (Cardinale et al., 2012; van der Plas, 2019). However, it is often hard to translate these findings into specific policy and management-relevant recommendations, or use them to quantify how biodiversity affects people's quality of life (Manning et al., 2019; Srivastava & Vellend, 2005). One reason for this is that the link between ecosystem functioning and human social systems is rarely established. Another is that species richness, or other measures of biodiversity, are difficult to link to the roles and functions of individual species, making the species that provide ecosystem services hard to pinpoint, and thus manage. To address these shortcomings, the conceptual links between individual species and their interactions, ecosystem processes and the NCP that people value need to be more rigorously established (Cardinale et al., 2012; Potschin-Young et al., 2018).

In "real-world" (i.e., naturally assembled) ecosystems, many of the links between species and NCP supply are indirect and mediated by species interactions, making it difficult to determine how NCP supply is related to biodiversity (Mace et al., 2012; Ricketts et al., 2016). This is particularly evident for many regulating NCP that emerge from species interactions that span different trophic levels (e.g., pest control, seed dispersal and pollination) (Díaz et al., 2018; Lavorel et al., 2013). Adopting principles of network theory can help us to manage this complexity (Schleuning et al., 2015) and to quantify the contributions of individual species to NCP supply. By using an ecological network approach, one can track the interactions between species across trophic levels, quantify the frequency of such interactions in entire ecological communities, and measure the direct and indirect contributions of species to NCP supply (Keyes et al., 2021; Reiss et al., 2009). We argue that such network-based assessments can fundamentally improve estimates of how many species are required for the supply of material and non-material NCP, and how important each of these species are for NCP supply.

In this study, we present a conceptual framework, which we term the "network cascade" framework. In it, we adapt the existing cascade model structure for ecosystem services, which describes the cascade through several organizational levels (biophysical environment, ecosystem functions, and ecosystem services to human benefits) to match the NCP paradigm. This allows NCP to be placed in line with much of the ecosystem services literature as the cascade model forms the basis of much ecosystem services accounting, including the natural capital approach (Bateman & Mace, 2020). By placing the complexity of species interactions within ecological networks in the biophysical component of this model, we expand on previous frameworks and can quantify the contributions of individual species to NCP supply. The resulting approach generates more specific information about the role of biodiversity in the supply of NCP than that provided by existing approaches.

Our integrated framework presents the flow of NCP supply from ecosystems to people as comprising three main elements (Figure 1): the social system that defines human demand for different NCP, the organisms that supply NCP directly or indirectly via their interactions in ecological networks, and the abiotic and biotic conditions that ultimately support these organisms. We demonstrate how the framework can be applied to social and ecological data by using both simulated and real-world data. With these examples, we show how the framework can be used to identify which and how many species are required for the supply of a specific NCP and to address two key questions:

1. How do differences in human demand for NCP influence the importance of biodiversity to people, and the identity of species that are important? We hypothesize that a diversified NCP demand requires a larger number of species to underpin NCP supply.
2. How do differences in species interactions across trophic levels modulate the importance of biodiversity to people? We hypothesize that NCP provided by specialized interactions require more species than NCP underpinned by networks dominated by generalist species.

THE FRAMEWORK AND ITS COMPONENTS

Our "network cascade" framework extends the cascade model introduced by Fisher et al. (2008) and later refined by Potschin and Haines-Young (2011). The cascade model describes the cascading flows that connect nature to people, with connections running from the environment to ecosystem processes, and then to ecosystem services (here NCP), final benefits, and human well-being. We retain these core features, but introduce a perspective change where the flow originates from stakeholder demand for NCP and cascades backwards into the natural elements that provide them (Figure 1). We believe that this emphasis on human demand focuses our search for the species providing NCP, making them easier to identify, and providing a new perspective of how biodiversity underpins NCP supply.

The "network cascade" framework is based around three core components (visualized as coloured boxes in Figure 1): the socio-economic system, which determines NCP demand, the NCP providers and regulators, which are the main biotic actors of NCP supply, and the supporting environment, which contains the entirety of biotic and abiotic conditions that indirectly drive NCP supply. In our framework, the demand for specific nature-derived benefits, or avoidance of detriments, determines the scoring of NCP (Figure 1a) and of the organisms that underpin them. For example, material NCP demand is realized by the harvesting or consumption of species, or products derived from species (Díaz et al., 2018). Importantly, the species that directly supply material NCP interact with many other species, the NCP regulators, and these interactions can enhance or limit NCP supply (Reiss et al., 2009). For example, crop plants interact with numerous pests and animal mutualists above and below-ground, with both positive and negative impacts on crop yield (Smith et al., 2021). Hence, by demanding the presence or absence of one NCP provider species, stakeholders will indirectly demand the presence or absence of many other regulating species, whose interactions determine NCP supply. In the framework, human demand therefore cascades onto the NCP providers and species which regulate NCP supply (Figure 1b).

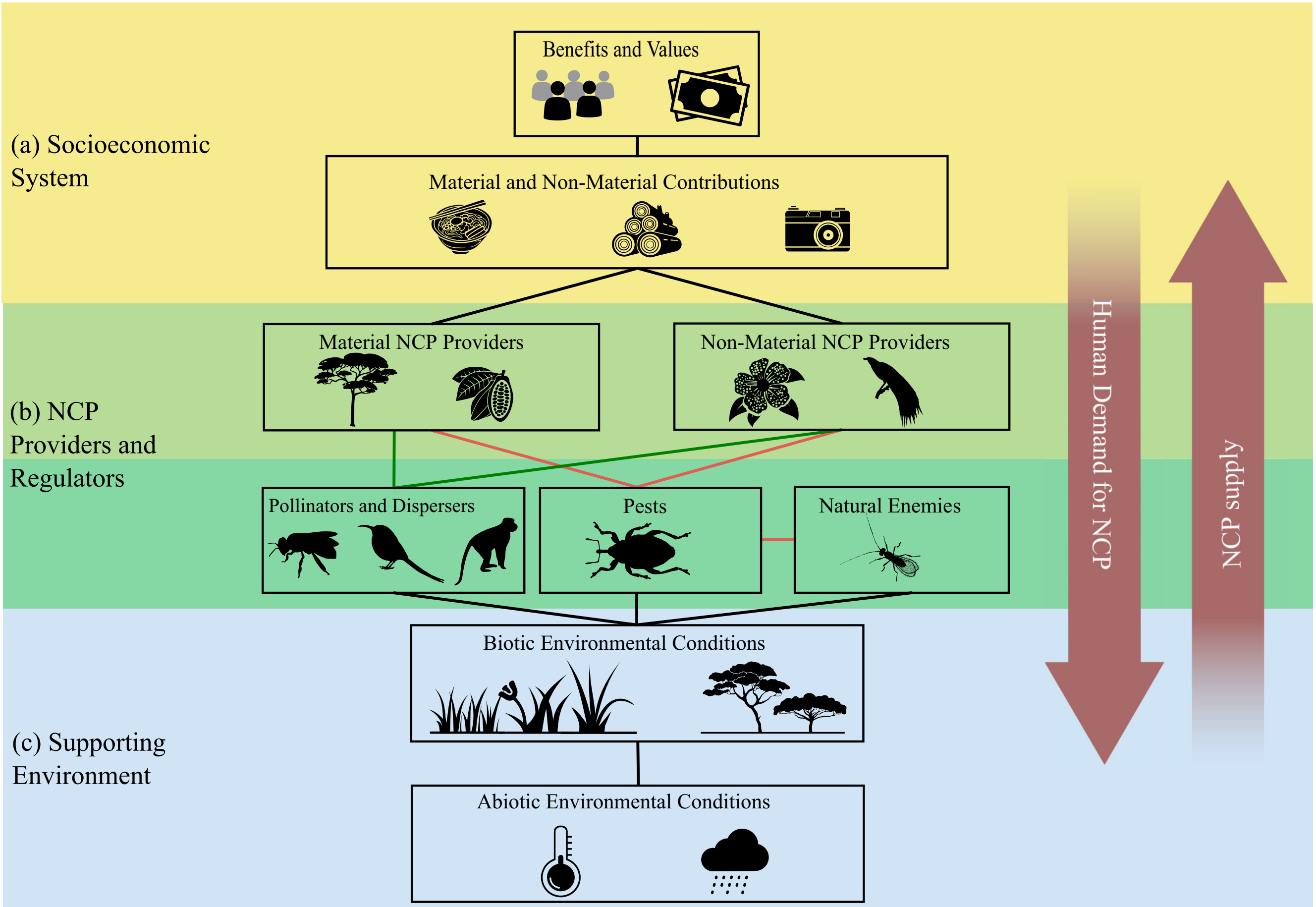

FIGURE 1 The "network cascade" framework. Shown is the cascading flow (black links) of human demand for NCP that is propagated through species interactions in ecological networks and extends to specific biotic and abiotic habitat conditions that support these species. The framework is divided into three main components. (a) The human demand for NCP; social or material values dictate NCP demand by stakeholders within the socioeconomic system. (b) Biotic interactions; the demand for NCP is linked to the organisms that provide them (e.g., crops and charismatic species) and to the organisms that regulate this NCP supply (e.g., pollinators, seed dispersers, natural enemies). NCP providers and regulators (light green and dark green, respectively) are linked by different types of interactions (green, mutualistic; red, antagonistic). (c) Habitat provision; the provider and regulator species depend on certain biotic and abiotic conditions provided by the supporting environment. By using this framework, it is possible to trace how the human demand for NCP translates into demand for specific provider and regulator species and, ultimately, into a demand for specific features of the supporting environment (e.g., deadwood, vegetation structure, geological features or climatic conditions). Vertical arrows across the three building blocks of the framework define the intertwined nature of the "network cascade" framework, with flows going downwards from people to nature and upwards from nature to people.

At the lowest level of the cascade, the framework considers the biotic and abiotic environmental conditions that are required to support the NCP providers and regulators. This allows us to determine the environmental conditions that support an NCP (Figure 1c) and, ultimately, how changes in environmental conditions will alter NCP supply. In the following sections, we will explain the main processes shaping each of the three framework components, and how these processes can be quantified.

Demand for NCP

Stakeholders' demands define the identity and amount of NCP needed or desired by individuals, groups and society (Linders et al., 2021; Villamagna et al., 2013). A range of approaches can be employed to measure NCP demand (Wolff et al., 2015). These include questionnaire surveys in which relative priority scores are assigned to a range of NCP (Linders et al., 2021; Peter et al., 2022; Washbourne et al., 2020). When implementing this framework, such relative priority scores can be used as quantitative estimates of the demand of each NCP, or NCP provider species. If the study is performed on a single NCP (e.g., crop production), then it is appropriate to obtain lists of used species and quantify priority scores based on the relative importance of the different contributing species. Where social survey data are not available, the demand may be estimated from existing patterns of NCP use or consumption (Wolff et al., 2017) or simulated in scenarios, representing the expected demand patterns of different stakeholder groups (e.g., Allan et al., 2015; Neyret et al., 2021). Potential changes in demand, as caused by policy, economic and environmental changes can also be simulated by implementing different scenarios of expected change in demand scores (Neyret et al., 2023).

NCP Providers and Regulators

In our framework, organisms involved in the direct supply and indirect regulation of NCP are termed NCP providers and NCP regulators, respectively. We define species that directly supply final contributions to people as NCP providers, following Kremen (2005). Examples of NCP providers include cultivated crops, wild plants and animals harvested for food or other uses, disease organisms of humans, and charismatic species valued for cultural reasons. An individual NCP can be supplied by a single or multiple provider species. Accordingly, in the framework, each provider species is assigned a score based on its current contribution to NCP supply.

The supply of NCP from providers in turn depends on their multiple interactions with species that control the underlying regulating NCP, which we term NCP regulators. In our framework, the many interactions between NCP providers and regulators are described by an interaction network, where nodes represent species, and the links depict the strength and nature of the interactions connecting different species (Bascompte & Jordano, 2007). The values of the links, which represent the quantitative dependence of NCP supply on NCP regulators, can be estimated via measures of interaction strength (Bascompte & Jordano, 2007; Wootton & Emmerson, 2005). Interaction strength can be quantified from direct observations of interacting species (Vázquez et al., 2012) or inferred from indirect analysis, for example based on molecular analyses (Evans et al., 2016). Ultimately, the structure of this interaction network is given by the interactions between its constituting species and defines how the human demand for NCP providers cascades from NCP providers to NCP regulators. As interaction data are required, the framework is most applicable to cases where the contributions of regulator species to NCP supply are quantifiable. This may not be the case for NCP that result from largely unknown biotic interactions and/or a mixture of abiotic and biotic contributions (e.g., nutrient cycling or decomposition).

The Supporting Environment

NCP supply ultimately depends on the biophysical components of the ecosystems that support biodiversity (Díaz et al., 2018; Mace et al., 2012; Potschin & Haines-Young, 2011). In the framework, the environment supports the supply of NCP by providing suitable environmental conditions for NCP provider and regulator species. As a consequence, human demand for NCP can be traced down to the needs of provider and regulator species for certain environmental conditions. These conditions do not only include the abiotic conditions, such as climate, but also the physical properties of habitats that emerge from its constituting species. In difference to the NCP regulators, these biotic properties of the environment cannot be traced down to pair-wise interactions between species, but rather emerge from the composition of whole species assemblages. For example, various bee species are important in providing pollination services and depend on suitable nesting sites and the availability of specific materials to construct their nests (Westrich, 1996). In this case, the NCP provided by bee-pollinated crops depends on the presence of bee species and on the abiotic and biotic habitat conditions required by these bees. Another example is the provision of specific microhabitats to NCP providers and regulators, such as those provided by the presence of cavities, deadwood or epiphytic plants in forest ecosystems (Larrieu et al., 2018). We propose that such indirect contributions of environmental conditions to NCP supply can be evaluated with statistical models that relate the occurrence and abundance of provider and regulator species to specific environmental conditions or habitat conditions, for example, by using species distribution models (Elith & Leathwick, 2009) or hierarchical community models (Ovaskainen et al., 2017). By linking such models to our framework, the entire cascade from human demand for NCP down to the environmental conditions that support the NCP providers and regulators can be quantified.

QUANTITATIVE APPLICATION OF THE "NETWORK CASCADE" FRAMEWORK

In this section, we detail how to calculate importance scores that quantify the relative contribution of individual species to NCP supply within our framework. The NCP provider score measures the proportion of an NCP that is supplied by one NCP provider species. In a multi-NCP assessment, this score would be weighted according to the priority score this NCP receives from stakeholders, as determined by existing use patterns, or stated demand. At the regulator level, the NCP regulator score quantifies the contribution to NCP supply by one regulator species. At the environmental level, we can calculate a score to describe the importance of a specific environment (e.g., forest or grassland) or habitat feature (e.g., deadwood presence) in supporting a species of NCP provider or regulator. At each of these three levels, we can integrate these species-specific scores into measures of diversity, for example, to quantify the number of regulator species required to underpin NCP supply in a given community.

To present the score calculations at the base of the framework, let us consider a species community of j

provider species and k regulator species which rely on l habitat types. We use capital letters to indicate the scores and diversity indices calculated with the framework.

The NCP provider score is expressed as the proportional contribution (i.e., relative importance) of one species to NCP supply. The provider score P_j is obtained by dividing the amount of NCP supplied by a provider species (N_j) by the total NCP supply N provided by the entire community of provider species. P_j is multiplied by the relative priority scores that stakeholders give to a specific NCP, as in Equation (1). If the analysis is considering a single NCP, the NCP priority score equals 1.

$$P_j = \frac{N_j}{\sum_{i=1}^{j} N_i} \cdot \text{NCP priority score} \quad (1)$$

In our framework, the biotic interactions that link provider and regulator species are defined as $I_{j,k}$. We propose to measure $I_{j,k}$ as the interaction strength defined by the interaction frequency between j and k ($f_{j,k}$), divided by the sum of all interactions that provider j has with all k regulators, as in Equation (2).

$$I_{j,k} = \frac{f_{j,k}}{\sum_{i=1}^{j} f_{i,k}} \quad (2)$$

The score R of and individual regulator species k represents the relative importance of a regulator species for NCP supply within a species community. It is the given by the sum across of $I_{j,k}$ values, each weighted by the NCP provider score P_j as in Equation (3).

$$R_k = \sum_{i=1}^{j} I_{i,k} \cdot P_j \quad (3)$$

At the lowest level, we define the links between a regulator k and habitat l as habitat dependence, $U_{k,l}$. This is a proxy of how much an organism relies on a given habitat feature or environmental condition. For example, a value of $U_{k,l}$ of 1 indicates total dependence and 0 indicates no relationship between a species k and habitat l. The habitat provision score Z of habitat type l is given by the sum of the regulator scores weighted by the species-specific habitat dependence scores, as in Equation (4).

$$Z_l = \sum_{i=1}^{k} R_i \cdot U_{i,l} \quad (4)$$

At each of the three levels, we can calculate diversity metrics, for example, by calculating Shannon diversity H (Jost, 2006). For instance, we can calculate the Shannon diversity across the R_k of all regulator species, considering both the number of species and their relative contributions to NCP supply. Based on this, we can calculate the effective diversity required for NCP supply as the exponential of H (Jost, 2006). The same approach can be applied to estimate effective diversity at the levels of NCP provider species or habitat types.

APPLICATIONS OF THE "NETWORK CASCADE" FRAMEWORK

In this section, we show how the "network cascade" framework can be employed to quantify the contributions of NCP regulators and the environment to the supply of NCP via NCP providers. We present two example scenarios in which the relationship between biodiversity and NCP supply is different, in one case due to differences in human demand (Figure 2) and in another due to differences in interactions between NCP providers and NCP regulators (Figure 3). These scenarios exemplify how the "network cascade" framework can be used to test specific hypotheses, such as those stated above (see introduction), about the relationship between human demand, biodiversity and NCP supply. In both scenarios, we examine how food production (material NCP) is linked to pollination (regulating NCP), and the availability of pollinator habitats. Food production is supplied in different amounts by three plant provider species (top row Figures 2 and 3) whose importance scores are defined by stakeholder demand. Food production is conditional on crop pollination by NCP regulators. The interactions between plant and pollinators vary in frequency. At the lowest level, individual pollinators depend on different habitat types, in our example representing the main habitat types surrounding agricultural lands.

In the first example (Figure 2), we quantify the effects of stakeholder demand on NCP supply at the level of NCP regulators and habitat provision. When demand is restricted to mainly one organism (monoculture Figure 2a), the required effective diversity of NCP regulators is substantially lower than in a scenario where multiple species are demanded evenly (mixed crops, Figure 2b). In the monoculture scenario (Figure 2a), pollinators that interact with the dominant NCP provider are more important to stakeholders and little more than 50% of the available pollinator species are required. In turn, because the grassland habitat supports the most important pollinator species, grassland is four times more important to stakeholders than the forest habitat. In the mixed crops scenario (Figure 2b), the structure of the interaction network and habitat dependence are unchanged, but demand is spread evenly across the crop species. This strongly alters the relative importance of species and habitats. In line with our hypothesis, stakeholders now require an effective diversity of more than 80% of the available pollinator species, and the forest habitat is three times more important than in the monoculture scenario. In our worked example, the identity of the most relevant species is also affected by differences in demand: in the monoculture scenario, the bee is the

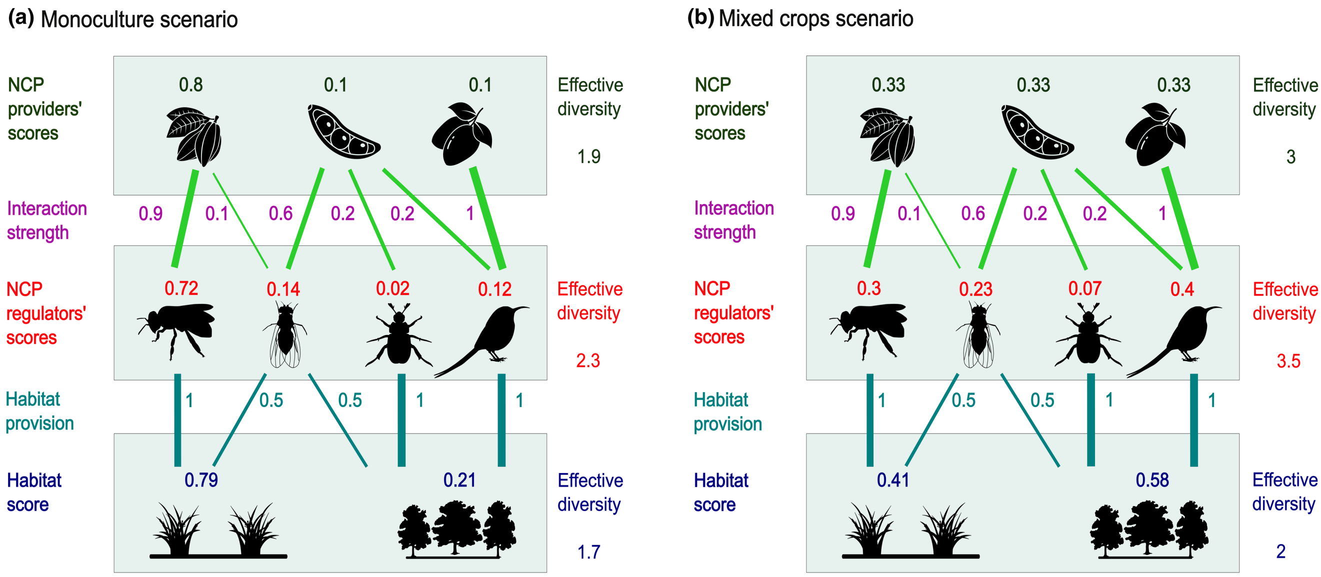

FIGURE 2 Stakeholder demands affect the relative importance of NCP regulators. A monoculture scenario (a) is contrasted with (b) a mixed crops scenario of three different crops. NCP providers are depicted in the top level, with their respective scores P_j (Equation 1) in green. Interactions between providers and regulators are indicated by light green links, with thickness reflecting the interaction strength values $I_{j,k}$ presented adjacently (equation 2). Regulators are depicted in the middle level, together with their respective scores R_k in red (Equation 3). NCP regulators are linked to supporting habitat conditions via turquoise links representing their habitat dependence ($U_{k,l}$). The lowest level depicts the habitat types supporting NCP regulators, with their respective habitat scores Z_l indicated in blue (Equation 4). Effective diversity corresponds to the exponential of the Shannon diversity calculated across the species or habitat scores at the respective level.

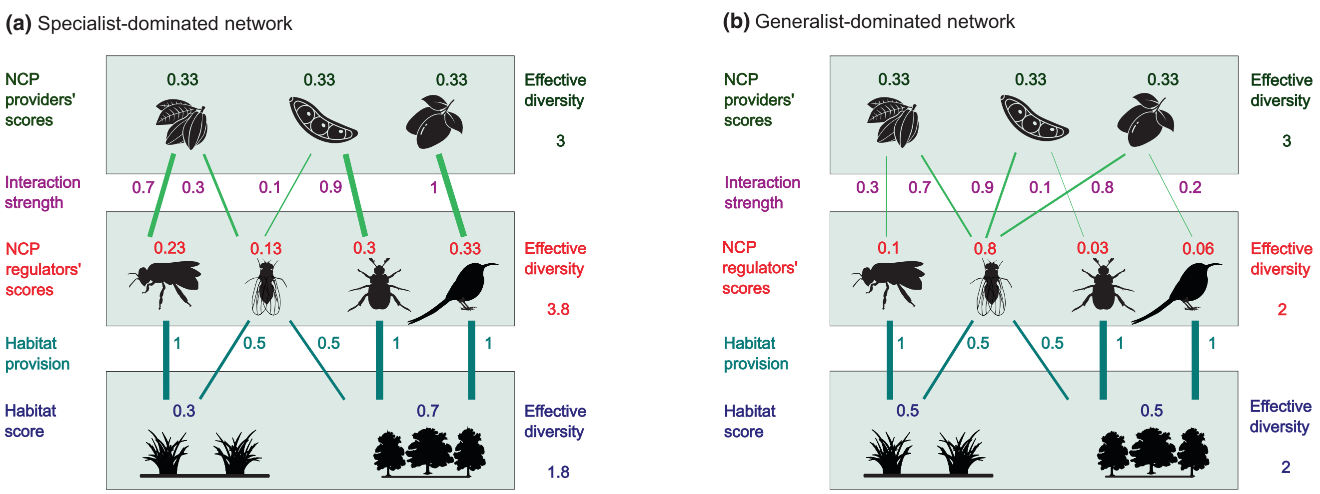

FIGURE 3 Changes in network structure affect the required diversity of NCP regulators. In (a) each crop is strongly reliant on a specific pollinator species, whereas (b) all crops are similarly dependent on a generalist butterfly species. NCP supply is identical to the scenario shown in Figure 2b. The respective scores and colour codes as well as the measure of effective diversity are explained in the caption of Figure 2.

most important, whereas in mixed cropping, the sunbird is the most important pollinator to stakeholders.

In the second example (Figure 3), we show how differences in network structure, and thus in the ecological components of the system, can modulate the importance of individual species and the biodiversity required to underpin NCP supply. We assess the role of network structure by altering the pair-wise interaction frequencies in the crop-pollinator network. In the first scenario (Figure 3a), each crop is predominantly pollinated by a specific specialist pollinator, whereas in the second scenario (Figure 3b), a generalist hoverfly pollinates most crops. As we hypothesized, in the specialist network, NCP supply is dependent on twice as many regulator species as in the generalist network (Figure 3). Differences in network specialization also affect the underlying habitat scores. In the first case, habitat importance is strongly determined by the number of how many specialist species it supports. Accordingly, the forest habitat is more important than the grassland in the specialist-dominated network (Figure 3a), whereas forest and grassland are equally important in the generalist network (Figure 3b).

APPLYING THE "NETWORK CASCADE" FRAMEWORK TO AN EMPIRICAL SEED-DISPERSAL NETWORK AND PLANT-BASED NCP SUPPLY

Here, we show how our framework can be applied to empirical interaction networks between plants and animals on Mt. Kilimanjaro (Vollstädt et al., 2018). We focus on plant-based NCP supply contributing to three material NCP: provision of food and animal feed, medicinal compounds and construction materials (Masao et al., 2022; Mollel et al., 2017). We compiled literature on the use of East-African plant species, some of which was obtained in social surveys, to determine which species were demanded for the three NCP (see Supplementary Information for the full list of references and a brief description of the approach taken). We then linked this human demand for individual plant species back to the NCP regulators underpinning these NCP by using network data that describe interactions between 40 fleshy-fruited plants and 68 animal seed dispersers (66 birds, two primates) (Vollstädt et al., 2018). As detailed data on plant use by people in the region, as a proxy of demand, are missing, we set the provider score P to 1 for all human used species. Using Equations (2) and (3), we then calculated a regulator score R for each seed disperser species by determining their proportional contribution to seed dispersal across all plant species. We then calculated the effective diversity of NCP regulators required for the supply of single and multiple NCP.

We found that generalist seed dispersers, like the common bulbul (*Pycnonotus barbatus* Desfontaine) and the blue monkey (*Cercopithecus mitis* Wolf), interact with many used plant species and contribute substantially both to single and multiple NCP. The presence of such species is therefore essential for NCP supply on Mt. Kilimanjaro. In addition, we found that certain tree species are dispersed by specialized species. The role of specialists becomes more prominent if demand was shifted towards specific NCP. If stakeholders were to prioritize the supply of medicinal compounds, which could be simulated by upweighting their provider scores, the mountain greenbul (*Arizelocichla nigriceps* Shelley) would become the most important seed disperser, while if demand for building materials were to increase, the large-bodied silvery-cheeked hornbill (*Bycanistes brevis* Friedmann) would gain the highest importance.

Overall, we found that each NCP requires a similarly high number of seed dispersers (about 25 species of animal seed dispersers for each NCP, see Figure 4). The simultaneous supply of all three NCP would require an effective diversity of 27 species, indicating that many species support more than one NCP. This case study demonstrates the applicability of the "network cascade" framework to real-world data on human demanded NCP and plant–animal networks. It further shows how such data can be used to identify the importance of individual regulator species across multiple NCP.

FUTURE DIRECTIONS

We foresee that our framework can be widely applied to different types of social and ecological systems. Nevertheless, we acknowledge limitations of our framework that require its further expansion if they are to be overcome. Here, we highlight the key limitations of our framework and suggest several possible extensions.

Co-Production of NCP

Human participation in the co-production of NCP is an important aspect of their supply (Díaz et al., 2015). Co-production can be thought of not only as inputs of non-natural capital, including financial and manufactured capital (Palomo et al., 2016), but also knowledge and labour investments that alter the supply of NCP. Existing conceptualizations of NCP co-production (e.g., Bruley et al., 2021) are conceptually compatible with the cascade model and co-production could be incorporated into our framework at various levels. For example, human contributions could be represented in the same way as individual species' contributions (e.g., 10% of pollination is done by hand), by the removal of species in management actions (e.g., the removal of pests with selective pesticides), or by knowledge changes that alter the demand and use of NCP providers (e.g., the use of an additional medicinal plant following education, altering its P score). Including co-production will provide more accurate information on the relative roles of humans and biodiversity in NCP supply. Such future studies could use this extended framework to test hypotheses relating to this, for example, that co-production inputs in agriculture reduce the effective diversity of species required to supply material NCP.

Integrating Multi-Trophic Complexity

Previous work has demonstrated that the removal of regulator species has different effects on ecosystem service supply depending on species' positions in multi-trophic food webs (Hines et al., 2015; Keyes et al., 2021). In our integration with the NCP framework, we have focused on ecological networks between two trophic levels. Nevertheless, the "network cascade" framework is well suited for incorporating elements of food web theory across multiple trophic levels. For example, the framework could be expanded using multi-layer network approaches, where different interaction types can be connected through shared resource species (Pilosof et al., 2017; Timóteo et al., 2023) This way, for example, it would be possible to account for the positive effects

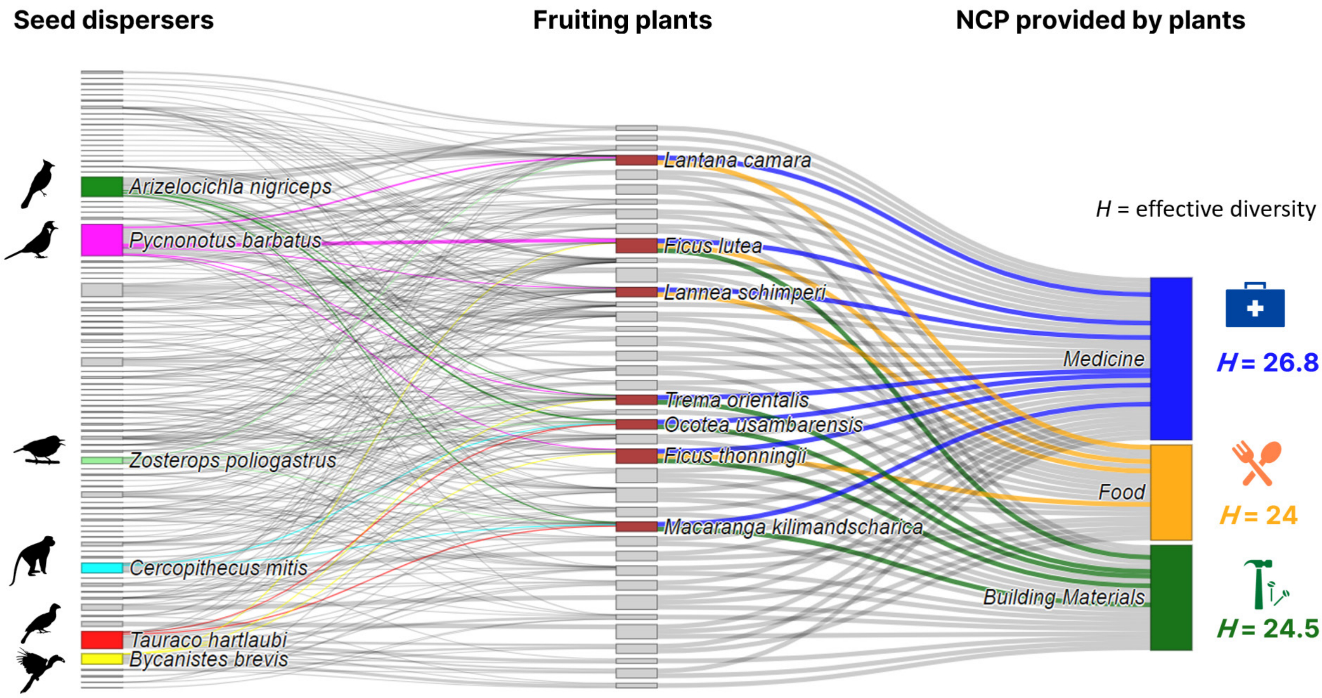

FIGURE 4 The seed-dispersal network underpinning the supply of plant-derived NCP on Mount Kilimanjaro. The figure shows interactions between seed dispersers (left) and fruiting plants (centre) and the plant-based NCP resulting from these interactions (right). Each plant species is linked to the NCP they underpin; medical compound species are pooled together and are shown in blue, food species are in orange and building material providers in dark green. The effective diversity of NCP regulators involved in the supply of NCP (H) is reported as a number under the respective NCP icon. The size of seed dispersers' nodes reflects their regulator score, R_k. The size of the plant nodes is determined by the number of NCP types they underpin. The size of NCP nodes reflects the number of plants species involved in their supply. To illustrate the information obtained by our approach, we highlight links between example species (in different colours) of animal dispersers and example plant species (in brown).

of pollinators on plant reproduction and simultaneously account for the negative effects of animal herbivores on the same plant species. Integrating the direct and indirect interactions across multiple trophic levels would provide a more comprehensive understanding of the diversity of species and interactions required to underpin NCP supply. However, such interaction data are time consuming and costly to collect (Pocock et al., 2012). In the absence of observed interactions, it may be possible to predict interactions and their frequencies based on trait-matching (Brousseau et al., 2018; Nowak et al., 2022), or assume interaction links between species from existing knowledge. Using such approaches in the future can serve to test the hypothesis that more species are required for the supply of those NCP that depend on interactions across multiple trophic levels.

Spatial and Temporal Changes in Network Structure and NCP Demand

In this paper, we demonstrate the use of the “network cascade” framework to investigate different scenarios of static network structure and NCP demand, but we suggest that our approach can be adapted to investigate changes in network structure and NCP demand, both in space and over time. By detailing how the identity of NCP providers and network structure changes across different ecosystems or ecoregions, one could compare the number and identity of species underpinning NCP supply in different places. Likewise, one could estimate the impact of changes in community composition and network structure over time, by assessing how interactions changed over multiple temporal snapshots, for example, to quantify how an invasive species might alter the effective diversity required for NCP supply. Similarly, it would be possible to investigate how differences in demand for, and use of, NCP among social-ecological systems, lead to changes in the number and identity of key species. One could also quantify how temporal changes in NCP demand and use, for example, afforestation of pasture and corresponding changes in service use, would lead to changes in the number and identity of the underlying NCP providers and regulators. Such applications of the framework could be used to test whether the demand for biodiversity increases with a diversified NCP demand at large spatial scales, and how the identities of key species are likely to change under future conditions. Information from such studies is increasingly needed to inform global policy and planning at the science–policy interface (Díaz et al., 2015; IPBES, 2019). However, we believe that it is important to clarify that deeming species or environmental conditions redundant or expendable in specific regions might be misleading. The suggested framework assesses species specifically in terms of their relative importance to stakeholders, and not as part of ecosystems as a whole. Species that are not involved in NCP supply might, nevertheless, be of fundamental importance for ecosystem stability under current and future conditions.

CONCLUSION

We here present the "network cascade" framework, a quantitative concept that integrates NCP and interaction network theory. Via this integration, it becomes possible to trace the dependency of human demands for NCP through ecological networks and down to the supporting environment. We demonstrate how this framework can be employed to quantify the identity and number of species and habitats required for NCP supply. In our examples, we show that differences in both the social and ecological system can lead to substantial changes in both the identity and diversity of species required for NCP supply. Applying the framework to simulated scenarios, we reveal that a diversified human demand requires a larger biodiversity to underpin NCP supply and that more specialized ecological systems require a larger number of species to fulfil the human demands for NCP. Through the application to empirical data, the framework provides a powerful and highly flexible tool to quantify how much biodiversity is needed to secure and maintain the human demands for specific NCP. By proposing this framework, we present a tool to conservationists and policymakers to assess which species are in most need of protection to ensure the supply of NCP in the future.

AUTHOR CONTRIBUTIONS

All authors developed the conceptual idea and designed the framework. GB analysed the data and contributed analysis methods. GB drafted the first manuscript draft. All authors contributed to revising and finalizing the text.

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PEER REVIEW

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/ele.14371.

DATA AVAILABILITY STATEMENT

The data of the empirical example is publicly accessible in the online repository PANGAEA https://doi.pangaea.de/10.1594/PANGAEA.896172. The code used for producing results is accessible at https://doi.org/10.5281/zenodo.10037289.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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