Linking biodiversity and nature’s contributions to people (NCP): a macroecological energy flux perspective

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Keywords

Ecosystem services, biodiversity models, ecosystem function, food web
Abstract

Linking biodiversity and the provision of nature’s contribution to people (NCP) remains a challenge. This hinders our ability to properly cope with the decline in biodiversity and the provision of NCP under global climate and land use changes. Here, we propose a framework that combines biodiversity models with food web energy flux approaches to evaluate and map NCP at large spatio-temporal scales. While energy fluxes traditionally links biodiversity to NCP locally, biodiversity models permit to extend these predictions across extensive spatial and temporal scales. Importantly, this novel approach has the potential to assess the vulnerability of NCP to the climate crisis and support the development of multiscale mitigation policies.

Current trends in evaluating Nature’s contributions to people (NCP)

Nature’s contributions to people (see Glossary) (e.g., plant pollination, carbon sequestration, food provision, and water purification) are highly sensitive to changes in biodiversity due to species invasion, extreme and long-term climatic changes, and anthropogenic disturbances [1,2]. Uncertainty about the future of NCP resulting from biodiversity change and their importance to human societies worldwide requires reliable models capable of predicting future NCP changes at large spatial scales [3,4]. Due to the complexity of processes and interactions that determine ecosystem functioning in response to biodiversity change [5], most approaches that aim to assess NCP provision are often very context-specific (but see [4,6]) and usually applied at regional spatial scales [7,8]. This hinders progress toward estimating the capacity to provide different types of NCP across larger spatial scales and highly dynamic landscapes, with changing species compositions of
Although useful tools for assessing NCP have been developed over the last 20 years, they mostly rely on statistical modeling using biophysical (e.g. land cover, soil properties, climate, [11]), social or species-based (e.g. [12]) data [13]. In this way, most NCP produced by biophysical processes and anthropogenic assets can be assessed and quantified, while valuable NCP produced through specific components of biodiversity are not adequately captured, remaining highly uncertain [4]. As an example, a critical and well-studied service, pollination, is often estimated at the global scale in terms of the area of habitat suitable for pollinators around crops or by correlations with pollinator diversity and abundance [14]. In contrast, pollination in nature is the outcome of a set of ecological interactions between pollinator and plant communities. It can be measured through the amount and quality of pollen on the stigma [14], or the number and diversity of pollinators [15,16], nevertheless these measurements are usually restricted to local spatial scales [17]. Similarly, biodiversity underpins the provision of many essential NCP (e.g. fruit and seed dispersion, crop damage, pollination, and pathogen control), but the complexity of its relationships with NCP requires consideration of the species interactions that determine ecosystem functions to predict future NCP responses to changes in biodiversity (but see [4,6]).

Integrating biodiversity forecasts into NCP at large spatial scales is a complex challenge that should be properly addressed, and directly associating declines in biodiversity with the lower provision of ecosystem services may lead to biases in spatial conservation planning, e.g., by overlooking species interactions or underestimating the contribution of common species [17–19]. At the same time, changes in land use in different landscapes directly influence ecosystems, species composition and interactions, making it difficult to quantify the biodiversity-NCP
relationship [20,21]. Some initiatives propose approaches to integrate biodiversity into NCP, but those focus on conservation purposes and assess a limited number of NCP (e.g. [22,23]). Here, we introduce an approach to integrate biodiversity data and species interactions into models, estimating NCP at macroecological scales - e.g. for continental or global analyses- using allometric scaling laws (Box 1, Figure 1). This approach can integrate future predictions from biodiversity scenarios, enabling forecasting of the future of NCP on a global scale. It will prove particularly useful for quantifying how NCP respond to environmental and anthropogenic drivers across long temporal and large spatial scales, as well as for assessing the vulnerability of NCP to the climate crisis and supporting the development of multiscale environmental policies [7].

Linking biodiversity to NCP: lessons from local scales

Biodiversity plays a central role in regulating the fluxes of energy and matter that determine ecosystem functions and ultimately NCP [24]. Energy fluxes represent the amount of energy flowing through the links connecting species and trophic levels and describe the energetic structure of communities [25]. These trophic links can be used as proxies to quantify multiple NCP driven by trophic interactions (Box 2), due to their direct relationship to ecosystem functions [25]. Thus, understanding how to calculate fluxes of energy opens up new opportunities for better evaluation and predictions of NCP. For example, by quantifying all energy fluxes between an agricultural pest species and its predators, we can assess the strength of pest control in an ecosystem. In a broader sense, energy fluxes provide an opportunity to link ecosystem functioning and NCP evaluation with food-web ecology, which addresses the underlying network of species interactions [26].
Factors such as the sensitivity of food webs to disturbances (network stability), and limitations on the transfer of biomass within trophic levels have a massive influence on the functionality of the ecosystem and should be considered when predicting future scenarios for NCP [26]. Despite its potential applications, this framework is tailored to estimate energy fluxes only at small spatial scales, typically for areas where experiments or individual measurements (e.g. species metabolic rates, species abundance) can be performed. Moreover, this framework relies on a set of ecological variables that are often accessible to ecologists locally: the list of occurring species, species biomasses and body masses, and the set of trophic interactions between the taxa of the focal community. However, for regional or continental scales, these input data can’t be experimentally sampled, which hinders the application of this energy-flux framework to predicting macroecological NCP. There are, instead, alternative ways to predict these variables needed for flux calculations at macroecological scales. Here, we propose a method for applying this approach at larger scales, where most conservation efforts take place.

Scaling up local estimations of NCP: biodiversity models as valuable tools

To evaluate energy fluxes and associate them with NCP at large spatial scales, a few challenges related to data acquisition must be overcome (see Box 1 for details): the low availability of data on species abundance and the identification and establishment of the trophic links. Despite significant gaps in biodiversity knowledge (e.g. for many tropical regions), significant progress has been made in predicting current and future species ranges and distributions. These biodiversity models (i.e. here referred to as any model that predicts biodiversity data, like abundance,
interactions, distribution) can fill in gaps in biodiversity data, providing a comprehensive representation of biodiversity, and their predictive capabilities (including species occurrence, abundance, traits and interactions) at regional, continental and global scales are becoming better and more precise [27]. Three types of biodiversity models are needed to scale up local estimations of NCP through fluxes: species distribution models, abundance models and interaction models. Distribution (predicting species occurrences) and abundance (predicting species abundance) models generate predictions in plots, communities, or grid cells as a function of a set of environmental covariates. These predictions can be extrapolated across space (e.g. to make a map) or time (e.g. project forward for the climate or land-use scenarios). Interaction models that predict the interactions between species, essential data for building the network topologies across space, are traditionally based on traits such as body mass [28] and recently started to incorporate abiotic variables [29,30]. Species interaction data can also be retrieved from global databases (e.g. Globi [31] or GATEWAy v.1.0 for trophic interactions [32]) containing information on various ecosystems and interaction types. While these databases may not document all the potential interactions of any given species, they provide a first and easily accessible source of data. Finally, algorithmic methods can reconstruct the missing parts of a network as soon as a reasonable amount of links were primarily identified [33–35]. A detailed protocol to infer species links for terrestrial ecosystems can be found in [36]. Together, these biodiversity models provide the information needed to calculate fluxes and therefore allow us to integrate biotic (e.g. species interactions, species distributions) and abiotic (e.g. environmental variables) factors into a spatially explicit assessment of NCP. Moreover, we can apply this framework also across different time scales, for
example, to predict future scenarios of NCP under different climatic and land use conditions.

The potential to integrate biodiversity models and energy fluxes

Global estimation of NCP remains quite coarse when compared to the advances made in evaluating biodiversity data at the same scale. By combining biodiversity information with energy fluxes, we expand our ability to predict NCP for the vast majority of areas where data is missing. As an example, abundance measurements, needed to evaluate the flux of energy between species, are usually rare and sparse [37], but trait-based biodiversity models are being developed to estimate average population abundances [38–40] and can account for bioclimatic/biophysical factors, making their use with species distribution models highly consistent. A key advantage of this integration is that the resulting flux calculation connects NCP to biodiversity and local environmental conditions through a predictive framework based on accessible biological and biophysical information. In our case study (Box 3) we focus on trophic links, but similar workflows can be developed for NCP resulting from non-trophic interactions (see Box 2). This approach can be implemented starting from a local grid cell (local ecological network), up to regional and continental scales. Besides exploring different time and spatial scales, the inclusion of species interactions, which can drastically alter NCP provision [26], allows circumventing a limitation from current studies. Factors such as invasive species and their interactions, responses of ecological networks to climatic conditions, species interactions within assemblages through time, and many others are crucial and should be considered.
Our approach also creates a bridge to the large set of theoretical methods offered by food web ecology that can be incorporated to further test the effect of various perturbations. It is, for instance, relatively straightforward to estimate how communities would respond to punctual disturbances (pulse perturbations) by calculating the resilience of the community based on the fluxes [41] or to assess the robustness of the estimated functions of species extinctions [42]. The loss of a species can trigger secondary extinctions, critically affecting not only the ecosystem functionality but also the robustness of the NCP provided [43]. The approach could also be used to anticipate and prioritize conservation actions by identifying key species supporting the entire future or present communities [44]. As such, the food web framework underlying our macroecological projection of NCP provides a valuable tool to connect theoretical ecology and conservation planning.

Opportunities for future scenarios

Over the past 50 years, most NCP have declined globally as a consequence of climate and land use alterations [17]. The integration of macroecological models (e.g. species distribution models) with energy flux modeling allows us to disentangle the long-term impacts of these alterations on the capacity to provide NCP and to project future scenarios. Although different future scenarios for climate and land use change are projected in macroecological models, we tend to overlook projections for NCP [45]. Our framework enables the integration of projections of environmental conditions to estimate what the future of NCP will be in a global context. For instance, increasing temperatures consistently impact local abundances of species [46], ecological network structure and trophic interactions [47,48]. Simultaneously, land-use change is causing a general decline in the abundance, diversity, and health
of species and ecosystems [49]. Together, land use and climate change are thus likely to be key drivers of variety, quantity and spatial distribution of NCP throughout time. Pollination contribution, for example, is facing a decline due to factors such as land-use change, pesticides, invasive species and climate change [50].

At local spatial and short temporal scales, impacts of human activities on biodiversity are usually associated with a decrease in ecosystem functions and stability, therefore reducing the provision of important NCP. Due to cascading effects, those impacts might increase at larger spatial and longer temporal scales, leading to complex cross-scale interactions [7]. In that way, the relationship between biodiversity, ecosystem functioning and NCP across different scales must be better understood to avoid poor forecasts of future supplies of NCP [7]. By using energy flux to access NCP, it is possible to monitor and predict the sources of changes (both in space and time), while disentangling the influence of ecological processes e.g. secondary extinctions and invasion of species.

Concluding Remarks

Quantifying NCP on large spatial and long temporal scales is an urgent matter and, to address that, a detailed understanding of the relationship between biodiversity, ecosystem functioning and NCP is needed. Here, we propose an applied framework to integrate biodiversity models and energy fluxes approaches, to improve our abilities to evaluate NCP through a macroecological perspective. This approach allows accounting for both biotic (e.g. species presence and interactions) and abiotic (e.g. environmental characteristics) factors when estimating NCP. We also show examples of how this integration opens new venues to address unresolved questions (see Outstanding Questions), as well as to improve
conservation policies, by helping us identify and predict future scenarios for areas of NCP provision.

Acknowledgements

We acknowledge funding by the ERA-Net BiodivERsA - Belmont Forum call (project FutureWeb); the Deutsche Forschungsgemeinschaft (DFG, German Research Foundation) project no. BR 2315/22-1.
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Box 1: General workflow

Our workflow is divided into 7 steps:

Step 1: Obtain the metaweb with potential species interactions.

Step 2: Obtain species distributions for the study area.

Step 3: Predict species density for each grid cell of the region of interest.

Step 4: Obtain the local ecological network by subsetting the metaweb based on estimated species occurrences.

Step 5: Calculate energy flux across the ecological network using species metabolic rates.

Step 6: Associate fluxes of energy and/or species densities to NCP.

The local network must be known to estimate fluxes. In general, local networks are obtained by subsetting the species list and interactions that occur within the region of interest, i.e. the metaweb. For the species list, different sources are available and can be used (e.g. IUCN - https://www.iucnredlist.org, GBIF -
The metawebs can be obtained directly from primary sources (e.g., TETRAEU - [51]) or by extracting from aggregated databases (e.g., GLOBI - [31]) the interactions for the taxonomic groups and the region of interest (Step 1). In order to subset the metaweb, local species occurrences need to be estimated from their large-scale distributions. Geographic limits based on expert opinion can be used to achieve this, possibly combined with species distribution models using occurrence data to further improve accuracy (Step 2). To calculate energy fluxes, and hence evaluate NCP, it is necessary to build predictive models for species abundance in order to obtain local estimates of species' biomasses. In contrast to estimations based on small-scale experiments, data such as species' biomasses and distribution can be derived at macroecological scales only through modeling. In particular, species' biomass, which can be predicted using species' body mass and environmental conditions [39,40] (Step 3). Local networks are assigned by combining the metaweb of species interactions with the occurrence of species on the grid cell (Step 4). Fluxes throughout the network are calculated based on species' metabolic rates (using allometric regressions) and biomasses. Fluxes of energy can be calculated for single species or an entire trophic level (e.g. herbivores or species feeding on specific prey), depending on the NCP of interest (Step 5). The NCP to be evaluated should be associated with an individual flux of energy or summed network fluxes. By summing all fluxes of energy across the grid cells we evaluate NCP across large spatial scales (Step 6).

Box 2: Energy fluxes to NCP

A diversity of contributions delivered by nature to people can be directly related to individual energy fluxes or to summed network fluxes. Associating NCP to
specific trophic links is straightforward and it is a way to determine the amount of energy necessary for the ecosystem to sustain the contribution from nature. To illustrate how NCP can be associated with energy fluxes in ecological networks, we identified and listed a few examples in Table 1:

<table>
<thead>
<tr>
<th>NCP</th>
<th>Link indicator (sum of energy fluxes)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pollination</td>
<td>plant - pollinator</td>
</tr>
<tr>
<td>Seed dispersal</td>
<td>seed - disperser</td>
</tr>
<tr>
<td>Pest regulation</td>
<td>pest - predator</td>
</tr>
<tr>
<td>Species invasion</td>
<td>invasive species - resource</td>
</tr>
<tr>
<td>Disease control (vector-control)</td>
<td>vector - predator</td>
</tr>
<tr>
<td>Fish production</td>
<td>prey - fish</td>
</tr>
<tr>
<td>Carcass removal</td>
<td>abundance of scavengers</td>
</tr>
<tr>
<td>Hunting</td>
<td>abundance of hunted species</td>
</tr>
<tr>
<td>Nutrient cycling (mineralization)</td>
<td>assimilation efficiency per link</td>
</tr>
<tr>
<td>Nutrient cycling (decomposition)</td>
<td>influx to decomposers</td>
</tr>
<tr>
<td>Carbon sequestration</td>
<td>metabolic demand of species</td>
</tr>
</tbody>
</table>

Table 1. Potential associations between NCP and trophic links in ecological networks.
Box 3: Case study: control of an agricultural pest in Europe

To demonstrate how the workflow described in the previous section can be applied, we show how to derive energy fluxes for vertebrates in Europe and, from this, how to obtain access to pest control provided by vertebrate predators on a vole species (*Microtus arvalis*) across the continent. The species checklist as well as the network topology for European vertebrates was obtained from the TETRA-EU database [51]. To obtain local communities, we used species distribution ranges from Maiorano et al. 2013 (which combined species’ extent of occurrence with their habitat requirements). To estimate species biomass density, we used a macroecological model similar to the one developed by Santini et al. [40]. We trained this model on the TetraDENSITY database [37] using as predictors macro-climatic (i.e. precipitation, temperature, primary productivity) and species-specific variables (i.e. body mass and phylogeny) to estimate species biomass densities locally. Climatic variables were obtained from CHELSA [52], whereas species body mass was from [53–55].

Using the network topology and the species’ density predictions from the species distribution models, we obtained, for each pixel, the local network as well as the local densities of species. From this, we settled metabolic losses using allometric equations [56] and estimated energy fluxes using the R package *fluxweb* [41]. From the matrix describing the fluxes among species, we then evaluated the NCP of interest. Pest control was calculated as the (standardized by mass) sum of all influxes (vole-predators) from each pixel (Figure I). More details about each step of the workflow for this case study can be found in Supplementary Material. Analyses were performed in the R programming language [57].
Figure I. Agricultural pest (Common Vole - *Microtus arvalis*) control contribution provided by vertebrate species mapped across the European continent. Map of the top-down pressure (associated with pest control) on *M. arvalis*, a rodent pest for agricultural fields across Europe.

Outstanding Questions

1. How do NCP capacity change across spatial scales?
2. How will NCP capacity be impacted in future scenarios, under climatic and land use alterations?

3. Which NCP provision we are overlooking because we don’t properly consider biodiversity data when estimating it?

4. What are the consequences of diversity loss or gain to different NCP provisions? Do cascading effects on energy fluxes across ecological networks play a role in determining NCP?

5. How can we best integrate biodiversity and NCP capacity into conservation plans?

Glossary

**Abundance models**: predictive models to estimate population abundance of species. Mostly based on species’ body mass, such models can also include species’ biological traits and environmental conditions.

**Food-web theory**: area from ecology that describes the trophic links between species in an ecosystem, defined by the flow of energy between different trophic levels.

**Interaction models**: Models that use species traits (e.g. body mass, diet) and abiotic variables to predict the existence of interactions between species.

**Metaweb**: an ecological network containing all the species that occur within the study area and all of their potential interactions.

**Nature’s contributions to people (NCP)**: all the positive and negative contributions of nature to people’s quality of life. There are 18 categories of NCP used in IPBES assessment.
**Network topology:** Structure of a network that connects links and nodes. In ecology, species usually represent the nodes that are connected through the links (e.g. energy links).

**Species distribution models:** Models to predict or infer species distribution patterns across spatial scales, accounting for biotic (e.g. species interactions) and abiotic (e.g. environmental) factors.

**Trophic links:** feeding interactions between species in an ecological network.

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**Figure 1:** How biodiversity models and food web tools can be integrated to access the provision of NCP at macroecological scales. Macroecological models and food web theory tools use different input data. The integration of these approaches allows the evaluation of NCP capacity, through the identification of relevant taxa or interactions between species, and their association with specific NCP. Moreover, the use of this approach can be applied to conservation planning and future predictions in terms of vulnerabilities of NCP capacities.