## Trends in **Ecology & Evolution**



## **Opinion**

# Linking biodiversity, ecosystem function, and Nature's contributions to people: a macroecological energy flux perspective

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At macroecological scales, the provision of Nature's contributions to people (NCP) is mostly estimated with biophysical information, ignoring the ecological processes underlying them. This hinders our ability to properly quantify the impact of declining biodiversity and the provision of NCP. Here, we propose a framework that combines local-scale food web energy flux approaches and large-scale biodiversity models to evaluate ecosystem functions and flux-related NCP at extensive spatiotemporal scales. Importantly, this approach has the potential to upscale ecosystem functions, assess the vulnerability of flux-related NCP to the climate crisis, and support the development of multiscale mitigation policies.

### From communities to ecosystem functions and Nature's contributions to people

The functioning of ecosystems is highly susceptible to changes in biodiversity and community composition induced by species invasions, extreme and long-term climatic changes, and anthropogenic disturbances [1]. As such, it becomes urgent to better understand how the response of ecosystems to perturbations at the community level will affect ecosystem functioning and, ultimately, NCP (see Glossary). Food web theory and the distribution of energy fluxes among species can be used to form mechanistic links among perturbations, biodiversity, community structure, and **ecosystem functions** [2–4]. Interestingly, the concept of energy flux could also be applied to estimate some potential NCP (hereafter referred to as 'flux-related NCP') and better integrate ecological processes into the provision of NCP. The set of potential NCP that can be estimated through this approach is related to community-level processes that directly depend on interspecific interactions, such as regulation of detrimental organisms or food production (see Table 1 and following section for correspondences between energy fluxes and fluxrelated NCP). For instance, in the Baltic Sea, community shifts led to a massive change in fish harvest, both in terms of species and biomass extracted [5], mirrored by shifts in energy fluxes [6]. As such, food web models can help reveal the causal mechanisms between environmental drivers, multi-species response, ecosystem functioning, and the associated supply of NCP [7].

Uncertainty about the future of NCP requires reliable models capable of predicting ecosystem functions and NCP changes at large spatial scales [8,9] for different scenarios of global change. However, due to the complexity of processes and interactions that determine ecosystem functioning in response to global change, most approaches that aim to evaluate ecosystem functions are often very context specific and usually applied at regional spatial scales [3]. This hinders progress toward estimating ecosystem functions and the supply of flux-related NCP across larger spatial scales and highly dynamic landscapes [10,11]. Useful tools for assessing NCP at macroecological scales have been developed over the past 20 years, mostly based on

#### Highlights

Evaluating and mapping ecosystem functions and associated Nature's contributions to people (NCP) across large spatial scales is complex.

One particular and often overlooked challenge is to integrate communitylevel processes, such as species interactions, into the evaluation of flux-related NCP supply, especially when working at macroecological scales.

This flux-related NCP evaluation could greatly benefit from advances in food web theory and statistical biodiversity modeling, which could simultaneously improve our understanding of the trophic interactions in ecological networks and the prediction of biodiversity across time ad space while accounting for abiotic drivers (climate and land use).

We propose a macroecological framework that integrates biodiversity models and energy flux theory to upscale ecosystem functions and predicts the associated supply of flux-related NCP.

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Table 1. A diversity of contributions delivered by nature to people can be directly related to individual energy fluxes or summed network fluxes<sup>2</sup>

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Categories of NCP <sup>b</sup> (IPBES)	NCP	Link indicator (sum of energy fluxes)
Pollination and dispersal of seeds and other propagules	Pollination	Fluxes between plant and pollinator
	Seed dispersal	Fluxes between plant and seed disperser
Regulation of climate	Carbon sequestration	Fluxes to primary producers
Formation, protection, and decontamination of soils and sediments	Nutrient cycling (mineralization)	Nonassimilated flux to decomposers (1–assimilation efficiency)
	Nutrient cycling (decomposition)	Influx to decomposers
Regulation of detrimental organisms and biological processes	Pest regulation	Fluxes between pest and predator species (predation pressure) standardized per biomass of pest species
	Control of species invasion	Fluxes between invasive species and resource
	Disease control (vector control)	Fluxes between vector and predator
	Carcass removal	Fluxes to carcass scavengers
Food and feed	Fish production	Fluxes between prey and fish
	Hunted species production	Fluxes to hunted species

<sup>&</sup>lt;sup>a</sup> Associating NCP with specific trophic links is straightforward and a way to determine the amount of energy necessary for the ecosystem to sustain the contribution from nature. The table illustrates the associations between flux-related NCP and trophic links in ecological networks, which represent an estimate of the potential supply of these flux-related NCP.

<sup>b</sup>The categories of NCP shown were extracted from [53].

statistical modeling using biophysical (e.g., land cover, soil properties, or climate [12]), social or species-based (e.g., [13]) data [14]. In this way, most NCP derived from biophysical processes (e.g., carbon storage or prevention of soil erosion) and anthropogenic assets can be assessed and quantified, whereas flux-related NCP (e.g., pest regulation or fish production, but see Table 1 for more examples), which depend on the response of communities to different ecological drivers and the complex set of retroactions occurring because of species interactions, are not adequately captured and remain uncertain [9]. Here, we provide an integrative framework based on energy fluxes to upscale the estimation of ecosystem functions to large geographical scales and access the ecological supply of flux-related NCP [15], which represents the potential capacity of ecosystems to provide these NCP [16]. The approach we propose combines biodiversity data and species interactions into predictive models (Box 1 and Figure 1) to upscale energy fluxes for continental or global analyses. These models also offer the possibility to integrate future predictions from biodiversity scenarios, enabling forecasting of the future of ecosystem functions and flux-related NCP. Importantly, we emphasize that this framework does not incorporate NCP demand or the role of humans in the co-production of NCP. Appropriate transformation of potential capacity into realized supply, needed for decision and action, would require further work and could be a rewarding research area.

## The biodiversity-ecosystem functions-NCP relationship: lessons from local

Biodiversity has a central role in regulating the fluxes of energy and matter that determine ecosystem functions and, ultimately, flux related-NCP [17]. At the local scale, calculation of energy fluxes allows for improved estimations of the effect of community structure [18] and environmental conditions [19,20] on multiple ecosystem functions simultaneously (multifunctionality). Therefore, it is often seen as a way to mechanistically study the interplay between biodiversity and ecosystem functioning, while taking a holistic approach that integrates the complexity of communities [2]. Similar types of question can be addressed when fluxes are associated with NCP. For example,

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the sum of energy fluxes associated with a fish species quantifies its biomass production, which can be used to estimate food provisioning from that species [7]. Similarly, quantifying the fluxes between an agricultural pest species and its predators provides an estimate of predation pressure on the pest species, which is a proxy for the strength of pest control at the moment the biodiversity data were sampled. Furthermore, this approach enables the incorporation of factors such as the sensitivity of food webs to disturbances (network stability [19]) and limitations on the transfer of biomass within trophic levels, which have a massive influence on the functioning of ecosystems and should be considered when predicting scenarios for flux-related NCP [21]. Typically, this use of energy fluxes to quantify ecosystem functions is tailored to estimate energy fluxes only at small spatial scales, usually for areas where experiments or individual measurements (e.g., species abundance or body masses) 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 cannot be directly sampled, which hinders the application of this energy-flux framework to predicting ecosystem functions at macroecological scales.

### Scaling up local estimations of ecosystem functions: biodiversity models as valuable tools

To evaluate energy fluxes and associate them with ecosystem functions and flux-related NCP at large spatial scales, challenges related to data acquisition must be overcome (Box 1), namely the low availability of data on species abundance and the identification and establishment of relevant 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 [22]. These biodiversity models (referred to here as any model that predicts biodiversity data, such as abundance, interactions, and distribution) can fill in gaps in biodiversity data, providing a comprehensive representation of biodiversity, and their predictive capabilities (including species

#### Box 1. General workflow

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.

In general, local network topologies 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) or GBIF1). The metawebs can be obtained directly from primary sources (e.g., TETRAEU [54]) or by extracting from aggregated databases (e.g., GLOBI [28]) the interactions for the taxonomic groups and the region of interest (Step 1). To subset the metaweb, local species occurrences need to be estimated from their large-scale distributions. Geographical 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 to obtain local estimates of species biomasses. Data such as species biomasses and distributions can be derived at macroecological scales only through modeling. This is particularly relevant for species biomass, which can be predicted using species body mass and environmental conditions [36,37] (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 that also incorporate temperature) and species biomasses arising from environmental conditions. 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 fluxes of energy across the grid cells, we can evaluate NCP across large spatial scales (Step 6). A workflow example on how to apply these steps is presented in the supplemental information online, associating the trophic control exerted by a natural predator on a crop pest species (Figure I).

#### Glossarv

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

Ecosystem functions: biological, chemical, and physical processes operating in an ecosystem that contribute to its stability and resilience (e.g., herbivory or productivity).

Flux-related NCP: set of NCP specifically derived from energy fluxes within species interactions (see Table 1 in the main text for examples).

Food web models: characterize trophic interactions within an ecosystem to quantify energy fluxes between the different ecological groups.

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

Metabolic rate: energy expended by an organism over a given period of time. Metaweb: ecological network containing all the species that occur within the study area and all of their potential interactions. The elaboration of the network is usually based on species interactions previously described in the literature based on expert knowledge or field guides.

Nature's contributions to people (NCP): all the positive and negative influences of Nature on people's quality of life. There are 18 categories of NCP used in Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES)

Network topology: structure of a network that connects links and nodes. In ecology, species usually represent the nodes, which are connected through the links (e.g., energy links).

Species distribution models: predict or infer species distribution patterns across spatial scales, accounting for biotic (e.g., species interactions) and abiotic (e.g., environmental) factors. Trophic link: feeding interactions between species in an ecological network.



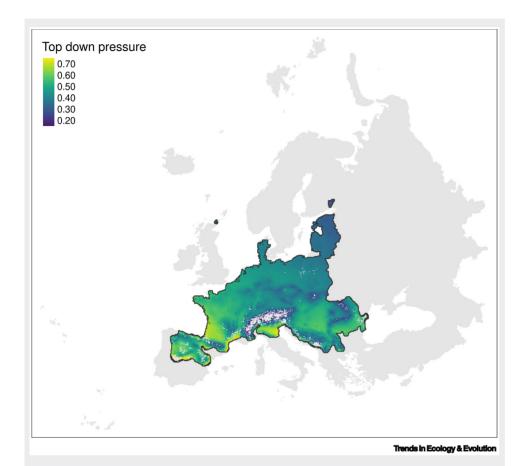


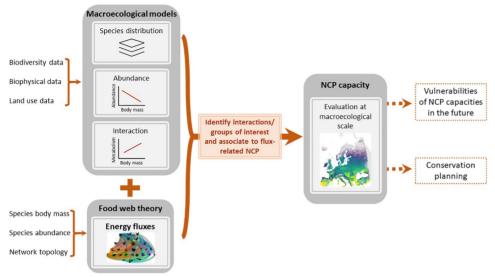
Figure I. Contribution of vertebrate species to the control of an agricultural pest (common vole, *Microtus arvalis*) mapped across the European continent. Map of the top-down pressure (associated with pest control) on *M. arvalis*, a rodent pest of agricultural fields across Europe (see also the supplemental information online). The lighter the color, the greater the top-down pressure. We emphasize that this result is intended to clarify how the framework can be applied to empirical data, and should not be used in further analysis or decisions.

occurrence, abundance, traits, and interactions) at regional, continental, and global scales are becoming more precise [22]. Three types of biodiversity model are needed to scale up local estimations of ecosystem functions through fluxes: **species distribution models**, **abundance models**, and **interaction models**.

Distribution (predicting species occurrence) and abundance (predicting species abundance) models generate predictions in plots, communities, or grid cells as a function of a set of environmental covariates. Environmental conditions exhibit considerable variation across an area, impacting physiological processes and, consequently, biodiversity patterns (e.g., distribution and abundance). Biodiversity models can account for this variation depending on their application (e.g., spatial scale or environmental variables used) and on the availability of data for the area [23]. The data sources used are also vital, and their availability will vary according to the location of the study area [24]. Therefore, environmental data should be carefully considered when predicting biodiversity patterns. These predictions can be extrapolated across space (e.g., to regions outside the extent of the original biodiversity data) or time (e.g., projected for future climate or

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Figure 1. How biodiversity models and food web tools can be integrated to access the provision of flux-related Nature's contributions to people (NCP) at macroecological scales. Macroecological models and food web theory tools use different input data. The integration of these approaches allows the evaluation of ecosystem functions at large spatial scales. Through the identification of relevant taxa or interactions between species, we associate ecosystem functions with the potential supply of flux-related NCP.

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 [25], and recently started to incorporate abiotic variables [26,27]. Species interaction data can also be retrieved from global databases (e.g., GloBI [28] or GATEWAy v.1.0 for trophic interactions [29]) 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 are primarily identified [30-32]. A detailed protocol to infer species links for terrestrial ecosystems can be found in [33]. Together, these biodiversity models provide the information needed to calculate fluxes and, therefore, allow us to integrate biotic (e.g., species interactions and distributions) and abiotic (e.g., temperature, land use type, and resource availability) factors into a spatially explicit assessment of ecosystem functions. Moreover, we can also apply this framework across different time periods to assess, for example, ecosystem functions and predict future scenarios of flux-related NCP under different climatic and land-use conditions.

This incorporation of community information in the estimation of flux-related NCP comes at the cost of a more complex approach relying on different models, each based on a set of parameters suffering two limitations. First, each model is associated with a level of uncertainty that can percolate through the other models until the final predicted fluxes. However, it is possible to estimate this effect on final predictions through a bootstrapping approach (Box 2), which can also be used as a sensitivity analysis to test the importance of any parameter or process. Second, there is a bias in availability (toward low-latitude regions and vertebrate species, especially birds) and quality of biodiversity data [24] to inform the ecological models regarding the true species distributions. For example, the absence of information regarding species distributions constrains the effective utilization of species distribution modeling (SDM). To address this limitation, it is possible to combine



#### Box 2. Model uncertainty and validation

The accuracy of the flux estimations directly relates to the precision of the estimated parameters and the performance of the model used. A potential way to account for such uncertainty is through a bootstrapping approach, which can be used to generate a distribution of energy fluxes, rather than a single value, for each link of a local food web, thus describing the whole uncertainty due to modeling choices. By repeating the sampling and evaluating the estimated flux each time, we can obtain a distribution of flux for each trophic link of the food web and, therefore, an average prediction and associated uncertainty.

For species distribution models, different approaches exist to propagate uncertainty and enforce decisions [55]. One possibility is to associate species with a probability of occurrence based on the output of distribution models and to draw random realizations of species occurrences from a Bernoulli process. The level of uncertainty can then be quantified by evaluating the consensus among several distribution models. For instance, considering a species to occur only when there is agreement among all models will result in a more restrictive scenario compared with evaluating species occurrence based on a majority consensus. Estimations of species abundances usually rely on quantitative models based on statistical regression [35-37], from which it is possible to obtain, for each species, a probabilistic error function that can be used to sample a predicted abundance. Finally, occurrences of trophic links can be weighted using a probability of realization by quantifying species trophic niches [25,31] and then sampled using a Bernoulli process.

To validate our framework, one option is to compare the predictions obtained for an ecosystem function or NCP to what is measured in a few local sites, therefore estimating how good the model is at predicting: (i) the values of the specific function considered: and/or (ii) the trends observed in the values recorded at the different locations. Moreover, these confrontations between predictions and data can also be used to refine the hypotheses from the different models. Another option is to compare the predictions from our approach to other available modeling approaches at large spatial scales, whenever possible. This could be the case for not only well-studied or economically important flux-related NCP, but also new approaches that are continuously being developed for other NCP predictions. These comparisons can also help evaluate the importance of community composition and structure on the supply of flux-related NCP.

multiple models and data sources to increase model robustness or to incorporate expert knowledge and field observations to validate and refine model predictions. Furthermore, the approach upscales the evaluation of ecosystem functions and, therefore, quantifies the potential supply of flux-related NCP, which describes the capacity of the system to provide such contributions. The realized supply of flux-related NCP is not incorporated into this approach and would require further work, which could be a rewarding future research area.

#### The potential to integrate biodiversity models and energy fluxes

Large-scale studies assessing flux-related NCP still lack precision, especially when compared with the advances in evaluating biodiversity data at the same scale. By combining biodiversity information with energy fluxes, we expand our ability to predict flux-related NCP for areas where data are sparse or limited. Given that our framework incorporates different biodiversity models independently from each other, each step can be independently tested and validated. Therefore, the quality of final predictions can be tested in areas where data are available. As an example, abundance measurements, needed to evaluate the flux of energy between species, are usually rare and sparse [34], but trait-based biodiversity models are being developed to estimate average population abundances [35-37] and can account for climatic and biophysical factors. These abiotic parameters are also those used as inputs for species distribution models, making their integration consistent. In our workflow example (see the supplemental information online), we focus on trophic links, but similar workflows can be developed for NCP resulting from nontrophic interactions (Table 1). This approach can be implemented starting from a local grid cell (local ecological network), up to regional and continental scales. Moreover, the explicit consideration of food webs allows us to consider more finely how changes in community structures (e.g., distributions of species, their abundances, and metabolic rates across trophic levels) will affect ecosystem functions and flux-related NCP.

Our approach also creates a bridge to the large set of theoretical methods [38-41] offered by food web ecology, which can be incorporated into the approach to further test the effect of various perturbations. As an example, it is possible to estimate how communities would respond to disturbances

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by calculating the resilience of the community based on the fluxes [19] (i.e., how the community will recover from a disturbance) or to assess the robustness of the estimated functions to species extinctions [39]. In the future, the approach could also be used to determine areas with a critical role in NCP supply and to identify key species supporting communities [7,41]. The loss of key species can trigger secondary extinctions, critically affecting not only the ecosystem functioning, but also the robustness of the flux-related NCP provided [40]. However, we emphasize that, before any use for conservation or decision-making purposes, the approach should be properly validated (Box 2).

#### Opportunities for future scenarios

Over the past 50 years, most NCP have declined globally as a consequence of climate and landuse alterations [42]. Although different future scenarios for climate and land-use change are used to predict NCP [43], flux-related NCP are usually overlooked. Our framework combines a modular approach that allows the integration of different elements related to global change scenarios that will affect differently the outputs of the models used. For instance, land use and increasing temperatures not only consistently impact species distributions [44] and local abundances of species [45], but also directly impact energy fluxes [19], ecological network structure, and trophic interactions [46,47]. Simultaneously, land-use change drastically impacts ecosystems through fragmentation processes, decreasing soil quality and increasing the risk of erosion, leading to biodiversity loss and causing a general decline in the abundance, diversity, and health of species and ecosystems [48,49]. Together, land use and climate change are thus likely to be key drivers of the variety, quantity, and spatial distribution of flux-related NCP through time [50].

#### Concluding remarks

Over the past decades, different methods have been developed to map the provisioning of NCP. Georeferenced metrics and geographic information system (GIS)-based approaches are the most commonly used and can efficiently account for spatiotemporal patterns and processes when quantifying NCP supply [51,52]. In contrast to other methods, our approach accounts for both biotic (e.g., species presence and interactions) and abiotic (e.g., environmental drivers) factors to upscale ecosystem function estimations and quantify the potential supply of flux-related NCP. In a broader context, this framework can be used to disentangle the impacts of environmental drivers (e.g., climate and land-use change) and community-level processes arising from trophic interactions on ecosystem functions and the supply of flux-related NCP at regional and continental scales. Thus, we show how this integrative approach opens new avenues to address unresolved questions (see Outstanding questions), and to improve our capacity to predict future changes in the supply of these NCP in the context of global change.

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#### **Declaration of interests**

None declared by authors.

#### Resources

www.iucnredlist.org www.gbif.org

### **Supplemental information**

Supplemental information to this article can be found online at https://doi.org/10.1016/j.tree.2024.01.004.

#### Outstanding questions

How can we expect ecosystem functions, such as productivity or herbivory, to be impacted in future scenarios of climate and land-use change within different parts of the

Are we overlooking the provision of NCP because we have not properly considered community processes in our assessment?

What are the consequences of diversity loss or gain to different NCP provisions at large spatial scales?

How do cascading effects on energy fluxes across ecological networks impact the supply of NCP?

How can we best integrate community processes and NCP capacity into conservation plans?

What are the similarities and/or differences between the output of this approach and others that do not consider community effects when estimating similar flux-related NCP (e.g., pest regulation or pollination)?



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