

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

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19

## 20 Abstract

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

## 30 Current trends in evaluating Nature's contributions to people (NCP)

31 **Nature's contributions to people** (see Glossary) (e.g., plant pollination,  
32 carbon sequestration, food provision, and water purification) are highly sensitive to  
33 changes in biodiversity due to species invasion, extreme and long-term climatic  
34 changes, and anthropogenic disturbances [1,2]. Uncertainty about the future of NCP  
35 resulting from biodiversity change and their importance to human societies  
36 worldwide requires reliable models capable of predicting future NCP changes at  
37 large spatial scales [3,4]. Due to the complexity of processes and interactions that  
38 determine ecosystem functioning in response to biodiversity change [5], most  
39 approaches that aim to assess NCP provision are often very context-specific (but  
40 see [4,6]) and usually applied at regional spatial scales [7,8]. This hinders progress  
41 toward estimating the capacity to provide different types of NCP across larger spatial  
42 scales and highly dynamic landscapes, with changing species compositions of

43 communities [9,10]. Although useful tools for assessing NCP have been developed  
44 over the last 20 years, they mostly rely on statistical modeling using biophysical (e.g.  
45 land cover, soil properties, climate, [11]), social or species-based (e.g. [12]) data  
46 [13]. In this way, most NCP produced by biophysical processes and anthropogenic  
47 assets can be assessed and quantified, while valuable NCP produced through  
48 specific components of biodiversity are not adequately captured, remaining highly  
49 uncertain [4]. As an example, a critical and well-studied service, pollination, is often  
50 estimated at the global scale in terms of the area of habitat suitable for pollinators  
51 around crops or by correlations with pollinator diversity and abundance [14]. In  
52 contrast, pollination in nature is the outcome of a set of ecological interactions  
53 between pollinator and plant communities. It can be measured through the amount  
54 and quality of pollen on the stigma [14], or the number and diversity of pollinators  
55 [15,16], nevertheless these measurements are usually restricted to local spatial  
56 scales [17]. Similarly, biodiversity underpins the provision of many essential NCP  
57 (e.g. fruit and seed dispersion, crop damage, pollination, and pathogen control), but  
58 the complexity of its relationships with NCP requires consideration of the species  
59 interactions that determine ecosystem functions to predict future NCP responses to  
60 changes in biodiversity (but see [4,6]).

61 Integrating biodiversity forecasts into NCP at large spatial scales is a complex  
62 challenge that should be properly addressed, and directly associating declines in  
63 biodiversity with the lower provision of ecosystem services may lead to biases in  
64 spatial conservation planning, e.g., by overlooking species interactions or  
65 underestimating the contribution of common species [17–19]. At the same time,  
66 changes in land use in different landscapes directly influence ecosystems, species  
67 composition and interactions, making it difficult to quantify the biodiversity-NCP

68 relationship [20,21]. Some initiatives propose approaches to integrate biodiversity  
69 into NCP, but those focus on conservation purposes and assess a limited number of  
70 NCP (e.g. [22,23]). Here, we introduce an approach to integrate biodiversity data and  
71 species interactions into models, estimating NCP at macroecological scales -e.g. for  
72 continental or global analyses- using allometric scaling laws (Box 1, Figure 1). This  
73 approach can integrate future predictions from biodiversity scenarios, enabling  
74 forecasting of the future of NCP on a global scale. It will prove particularly useful for  
75 quantifying how NCP respond to environmental and anthropogenic drivers across  
76 long temporal and large spatial scales, as well as for assessing the vulnerability of  
77 NCP to the climate crisis and supporting the development of multiscale  
78 environmental policies [7].

## 79 Linking biodiversity to NCP: lessons from local scales

80 Biodiversity plays a central role in regulating the fluxes of energy and matter  
81 that determine ecosystem functions and ultimately NCP [24]. Energy fluxes  
82 represent the amount of energy flowing through the links connecting species and  
83 trophic levels and describe the energetic structure of communities [25]. These  
84 **trophic links** can be used as proxies to quantify multiple NCP driven by trophic  
85 interactions (Box 2), due to their direct relationship to ecosystem functions [25].  
86 Thus, understanding how to calculate fluxes of energy opens up new opportunities  
87 for better evaluation and predictions of NCP. For example, by quantifying all energy  
88 fluxes between an agricultural pest species and its predators, we can assess the  
89 strength of pest control in an ecosystem. In a broader sense, energy fluxes provide  
90 an opportunity to link ecosystem functioning and NCP evaluation with **food-web**  
91 **ecology**, which addresses the underlying network of species interactions [26].

92 Factors such as the sensitivity of food webs to disturbances (network stability), and  
93 limitations on the transfer of biomass within trophic levels have a massive influence  
94 on the functionality of the ecosystem and should be considered when predicting  
95 future scenarios for NCP [26]. Despite its potential applications, this framework is  
96 tailored to estimate energy fluxes only at small spatial scales, typically for areas  
97 where experiments or individual measurements (e.g. species metabolic rates,  
98 species abundance) can be performed. Moreover, this framework relies on a set of  
99 ecological variables that are often accessible to ecologists locally: the list of  
100 occurring species, species biomasses and body masses, and the set of trophic  
101 interactions between the taxa of the focal community. However, for regional or  
102 continental scales, these input data can't be experimentally sampled, which hinders  
103 the application of this energy-flux framework to predicting macroecological NCP.  
104 There are, instead, alternative ways to predict these variables needed for flux  
105 calculations at macroecological scales. Here, we propose a method for applying this  
106 approach at larger scales, where most conservation efforts take place.

## 107 Scaling up local estimations of NCP: biodiversity models as valuable 108 tools

109 To evaluate energy fluxes and associate them with NCP at large spatial  
110 scales, a few challenges related to data acquisition must be overcome (see Box 1 for  
111 details): the low availability of data on species abundance and the identification and  
112 establishment of the trophic links. Despite significant gaps in biodiversity knowledge  
113 (e.g. for many tropical regions), significant progress has been made in predicting  
114 current and future species ranges and distributions. These biodiversity models (i.e.  
115 here referred to as any model that predicts biodiversity data, like abundance,

116 interactions, distribution) can fill in gaps in biodiversity data, providing a  
117 comprehensive representation of biodiversity, and their predictive capabilities  
118 (including species occurrence, abundance, traits and interactions) at regional,  
119 continental and global scales are becoming better and more precise [27]. Three  
120 types of biodiversity models are needed to scale up local estimations of NCP through  
121 fluxes: **species distribution models, abundance models and interaction models.**  
122 Distribution (predicting species occurrences) and abundance (predicting species  
123 abundance) models generate predictions in plots, communities, or grid cells as a  
124 function of a set of environmental covariates. These predictions can be extrapolated  
125 across space (e.g. to make a map) or time (e.g. project forward for the climate or  
126 land-use scenarios). Interaction models that predict the interactions between  
127 species, essential data for building the **network topologies** across space, are  
128 traditionally based on traits such as body mass [28] and recently started to  
129 incorporate abiotic variables [29,30]. Species interaction data can also be retrieved  
130 from global databases (e.g. Globi [31] or GATEWAY v.1.0 for trophic interactions  
131 [32]) containing information on various ecosystems and interaction types. While  
132 these databases may not document all the potential interactions of any given  
133 species, they provide a first and easily accessible source of data. Finally, algorithmic  
134 methods can reconstruct the missing parts of a network as soon as a reasonable  
135 amount of links were primarily identified [33–35]. A detailed protocol to infer species  
136 links for terrestrial ecosystems can be found in [36]. Together, these biodiversity  
137 models provide the information needed to calculate fluxes and therefore allow us to  
138 integrate biotic (e.g. species interactions, species distributions) and abiotic (e.g.  
139 environmental variables) factors into a spatially explicit assessment of NCP.  
140 Moreover, we can apply this framework also across different time scales, for

141 example, to predict future scenarios of NCP under different climatic and land use  
142 conditions.

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

144 Global estimation of NCP remains quite coarse when compared to the  
145 advances made in evaluating biodiversity data at the same scale. By combining  
146 biodiversity information with energy fluxes, we expand our ability to predict NCP for  
147 the vast majority of areas where data is missing. As an example, abundance  
148 measurements, needed to evaluate the flux of energy between species, are usually  
149 rare and sparse [37], but trait-based biodiversity models are being developed to  
150 estimate average population abundances [38–40] and can account for bioclimatic/  
151 biophysical factors, making their use with species distribution models highly  
152 consistent. A key advantage of this integration is that the resulting flux calculation  
153 connects NCP to biodiversity and local environmental conditions through a predictive  
154 framework based on accessible biological and biophysical information. In our case  
155 study (Box 3) we focus on trophic links, but similar workflows can be developed for  
156 NCP resulting from non-trophic interactions (see Box 2). This approach can be  
157 implemented starting from a local grid cell (local ecological network), up to regional  
158 and continental scales. Besides exploring different time and spatial scales, the  
159 inclusion of species interactions, which can drastically alter NCP provision [26],  
160 allows circumventing a limitation from current studies. Factors such as invasive  
161 species and their interactions, responses of ecological networks to climatic  
162 conditions, species interactions within assemblages through time, and many others  
163 are crucial and should be considered.

164 Our approach also creates a bridge to the large set of theoretical methods  
165 offered by food web ecology that can be incorporated to further test the effect of  
166 various perturbations. It is, for instance, relatively straightforward to estimate how  
167 communities would respond to punctual disturbances (pulse perturbations) by  
168 calculating the resilience of the community based on the fluxes [41] or to assess the  
169 robustness of the estimated functions of species extinctions [42]. The loss of a  
170 species can trigger secondary extinctions, critically affecting not only the ecosystem  
171 functionality but also the robustness of the NCP provided [43]. The approach could  
172 also be used to anticipate and prioritize conservation actions by identifying key  
173 species supporting the entire future or present communities [44]. As such, the food  
174 web framework underlying our macroecological projection of NCP provides a  
175 valuable tool to connect theoretical ecology and conservation planning.

## 176 Opportunities for future scenarios

177 Over the past 50 years, most NCP have declined globally as a consequence  
178 of climate and land use alterations [17]. The integration of macroecological models  
179 (e.g. species distribution models) with energy flux modeling allows us to disentangle  
180 the long-term impacts of these alterations on the capacity to provide NCP and to  
181 project future scenarios. Although different future scenarios for climate and land use  
182 change are projected in macroecological models, we tend to overlook projections for  
183 NCP [45]. Our framework enables the integration of projections of environmental  
184 conditions to estimate what the future of NCP will be in a global context. For  
185 instance, increasing temperatures consistently impact local abundances of species  
186 [46], ecological network structure and trophic interactions [47,48]. Simultaneously,  
187 land-use change is causing a general decline in the abundance, diversity, and health



188 of species and ecosystems [49]. Together, land use and climate change are thus  
189 likely to be key drivers of variety, quantity and spatial distribution of NCP throughout  
190 time. Pollination contribution, for example, is facing a decline due to factors such as  
191 land-use change, pesticides, invasive species and climate change [50].

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

## 202 Concluding Remarks

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

212 conservation policies, by helping us identify and predict future scenarios for areas of  
213 NCP provision.

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## 349 Box 1: General workflow

350 Our workflow is divided into 7 steps:

351 Step 1: Obtain the **metaweb** with potential species interactions.

352 Step 2: Obtain species distributions for the study area.

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

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

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

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

359

360 The local network must be known to estimate fluxes. In general, local  
361 networks are obtained by subsetting the species list and interactions that occur  
362 within the region of interest, i.e. the metaweb. For the species list, different sources  
363 are available and can be used (e.g. IUCN - <https://www.iucnredlist.org>, GBIF -



364 <https://www.gbif.org>). The metawebs can be obtained directly from primary sources  
365 (e.g., TETRAEU - [51]) or by extracting from aggregated databases (e.g., GLOBI -  
366 [31]) the interactions for the taxonomic groups and the region of interest (Step 1). In  
367 order to subset the metaweb, local species occurrences need to be estimated from  
368 their large-scale distributions. Geographic limits based on expert opinion can be  
369 used to achieve this, possibly combined with species distribution models using  
370 occurrence data to further improve accuracy (Step 2). To calculate energy fluxes,  
371 and hence evaluate NCP, it is necessary to build predictive models for species  
372 abundance in order to obtain local estimates of species' biomasses. In contrast to  
373 estimations based on small-scale experiments, data such as species' biomasses and  
374 distribution can be derived at macroecological scales only through modeling. In  
375 particular, species' biomass, which can be predicted using species' body mass and  
376 environmental conditions [39,40] (Step 3). Local networks are assigned by  
377 combining the metaweb of species interactions with the occurrence of species on the  
378 grid cell (Step 4). Fluxes throughout the network are calculated based on species'  
379 metabolic rates (using allometric regressions) and biomasses. Fluxes of energy can  
380 be calculated for single species or an entire trophic level (e.g. herbivores or species  
381 feeding on specific prey), depending on the NCP of interest (Step 5). The NCP to be  
382 evaluated should be associated with an individual flux of energy or summed network  
383 fluxes. By summing all fluxes of energy across the grid cells we evaluate NCP  
384 across large spatial scales (Step 6).

## 385 Box 2: Energy fluxes to NCP

386 A diversity of contributions delivered by nature to people can be directly  
387 related to individual energy fluxes or to summed network fluxes. Associating NCP to

388 specific trophic links is straight forward and it is a way to determine the amount of  
 389 energy necessary for the ecosystem to sustain the contribution from nature. To  
 390 illustrate how NCP can be associated with energy fluxes in ecological networks  
 391 webs, we identified and listed a few examples in Table 1:

392

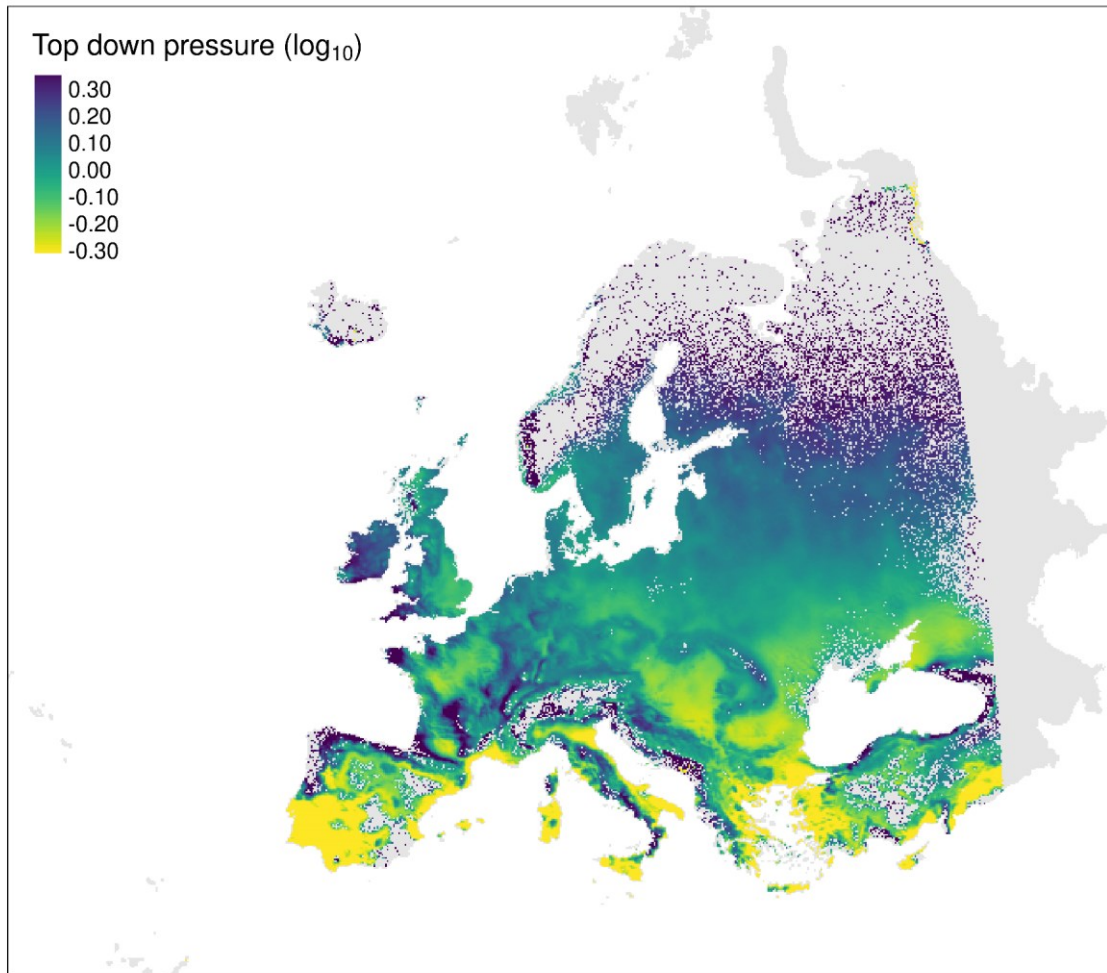
<b>NCP</b>	<b>Link indicator (sum of energy fluxes)</b>
Pollination	plant - pollinator
Seed dispersal	seed - disperser
Pest regulation	pest - predator
Species invasion	invasive species - resource
Disease control (vector-control)	vector - predator
Fish production	prey - fish
Carcass removal	abundance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

393 **Table 1. Potential associations between NCP and trophic links in ecological**  
 394 **networks.**

### 395 Box 3: Case study: control of an agricultural pest in Europe

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

410 Using the network topology and the species' density predictions from the  
411 species distribution models, we obtained, for each pixel, the local network as well as  
412 the local densities of species. From this, we settled metabolic losses using allometric  
413 equations [56] and estimated energy fluxes using the R package *fluxweb* [41]. From  
414 the matrix describing the fluxes among species, we then evaluated the NCP of  
415 interest. Pest control was calculated as the (standardized by mass) sum of all  
416 influxes (vole-predators) from each pixel (Figure I). More details about each step of  
417 the workflow for this case study can be found in Supplementary Material. Analyses  
418 were performed in the R programming language [57].



419

420 **Figure I. Agricultural pest (Common Vole - *Microtus arvalis*) control**  
 421 **contribution provided by vertebrate species mapped across the European**  
 422 **continent. Map of the top-down pressure (associated with pest control) on *M.***  
 423 ***arvalis*, a rodent pest for agricultural fields across Europe.**

424 Outstanding Questions

425 1. How do NCP capacity change across spatial scales?

- 426 2. How will NCP capacity be impacted in future scenarios, under climatic and  
427 land use alterations?
- 428 3. Which NCP provision we are overlooking because we don't properly consider  
429 biodiversity data when estimating it?
- 430 4. What are the consequences of diversity loss or gain to different NCP  
431 provisions? Do cascading effects on energy fluxes across ecological networks  
432 play a role in determining NCP?
- 433 5. How can we best integrate biodiversity and NCP capacity into conservation  
434 plans?

## 435 Glossary

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

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

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

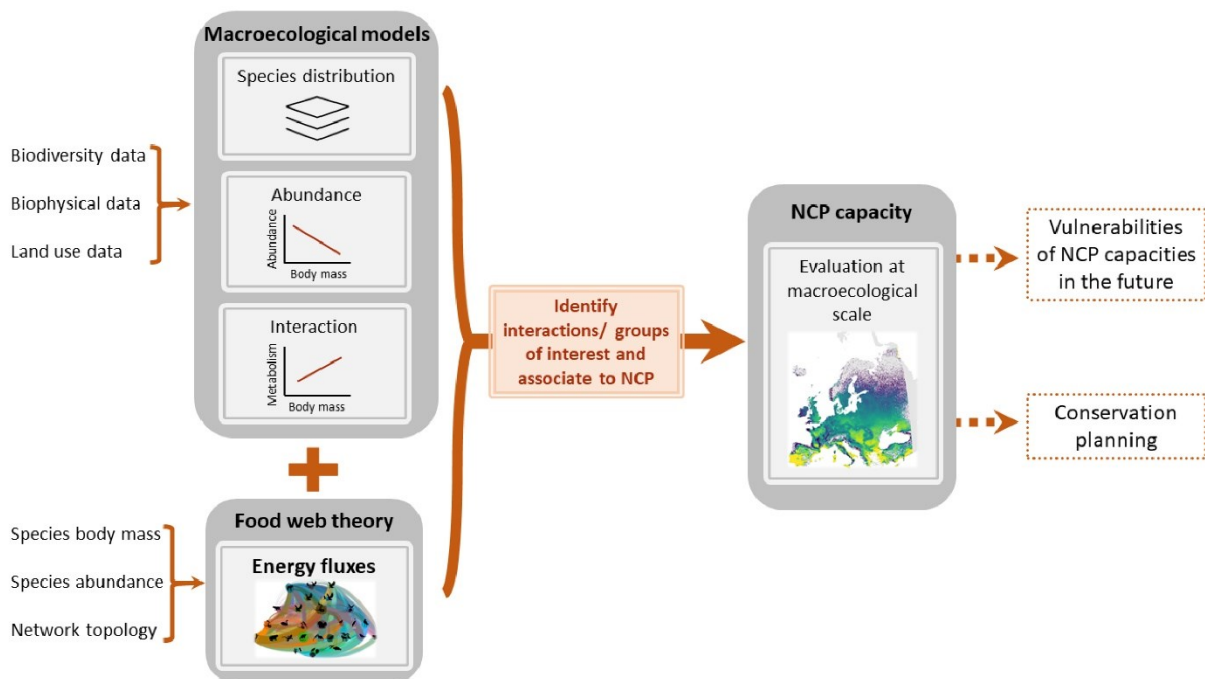
444 **Metaweb:** an ecological network containing all the species that occur within the  
445 study area and all of their potential interactions.

446 **Nature's contributions to people (NCP):** all the positive and negative contributions  
447 of nature to people's quality of life. There are 18 categories of NCP used in IPBES  
448 assessment.

449 **Network topology:** Structure of a network that connects links and nodes. In  
450 ecology, species usually represent the nodes that are connected through the links  
451 (e.g. energy links).

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

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



456

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

464