

RESEARCH ARTICLE

Identifying important species in meta-communities

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Abstract

1. With the ongoing biodiversity crisis, identifying which species are of particular importance to prevent the extinction of other species has become a pressing issue. However, most approaches to detect these important species are made at a local (i.e., community) level, without considering the potential effect of species dispersion in a landscape. As habitat fragmentation has important effects on biodiversity, we need methods to better assess how local and spatial processes interact to determine important species and therefore better inform conservation efforts.
2. We present a modified PageRank algorithm to determine the importance of species in meta-communities. Species importance is defined as the ability of species in the meta-community to spread nutrients within two sets of networks: food webs that depict local trophic interactions and landscape networks representing the movement of species across different habitat patches.
3. We show that dispersal and trophic links jointly determine the importance of the different species, both at the local scale (within habitat patches) and at larger scales (landscape). More precisely, we observed that (i) what is considered an important species changes between isolated communities and meta-communities and (ii) the importance of a species in a meta-community depends on the position of its habitat patch in the landscape network.
4. The importance of a species is influenced by both intrinsic factors (dispersal capacity, trophic position) and extrinsic factors (position of the patch in the landscape network). Our results stress the need for a larger-scale consideration of space in the identification of important species.

KEYWORDS

CheiRank, food web, key species, landscape networks, meta-communities, PageRank, species importance

1 | INTRODUCTION

In the context of the ongoing biodiversity crisis, predicting the effects of species extinctions on other species is a pressing issue.

In ecosystems, losing a species can lead to cascading effects on other species because of the complex set of ecological dependencies among species. For instance, after the loss of a species, some consumers can be left without further access to resources leading

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them to extinction (secondary extinction). Food webs represent a set of species and their trophic interactions and can be used to depict species inter-dependencies associated with their need for energy. Thus, they offer a valuable tool to identify which species are key to maintaining the energetic integrity of communities and minimise the number of secondary extinctions (Solé & Montoya, 2001). Several methods relying on food webs exist to identify important species. They usually rank species from the most important to the least important, defining an extinction order that will maximise the speed at which the food web collapses when species are sequentially going extinct following a given order (Dunne et al., 2002). The first species from such an arrangement are the ones that are key in limiting secondary extinctions and food web collapse. Although different methods follow a similar strategy, they can be classified into three different categories. First, species-focused methods consider information at the species level, defining importance based on the number of interactions a species has (Dunne et al., 2002). Second, local approaches consider the neighbourhood of species: important species are the ones with a high number of connections to other species being themselves connected to a high number of other species, this definition being potentially iterated to consider a more distant neighbourhood (Jordán, 2009). Third, global approaches consider the entire network to define species' importance. For instance, Allesina and Pascual (Allesina & Pascual, 2009) adapted the PageRank algorithm by Brin and Page (1998) to define species' importance by their ability to spread nutrients (energy) within the entire food web. This algorithm offers a reliable way to identify species whose extinctions lead to the collapse of the entire food web, thereby opening the possibility to optimise management plans which account for species interactions (McDonald-Madden et al., 2016). While species-focused and local approaches are based on link distribution only, the global approach, by making use of matrix algebra, already incorporates some implicit dynamical considerations (how nutrients spread in the network). Although correlated, the predictions from these various approaches exhibit some differences. Species-focused and local approaches predict that preserving highly connected and central species is important for limiting secondary extinctions (Dunne et al., 2002; Jordán, 2009). However, these species are not necessarily the best at spreading nutrients across food webs (Allesina & Pascual, 2009), so not necessarily the ones considered the most important by global approaches. As global approaches can predict the most efficient sequences of extinctions for food web collapse (Allesina & Pascual, 2009), as well as detect species having a strong influence on the biomass dynamics of other species (Frossard et al., 2018), these differences stress the importance of dynamical energetic consideration for identifying key species.

A common limitation of these approaches is that they consider ecological communities in isolation, that is, spatially disconnected from each other. Yet, individuals can disperse within landscapes and connect habitat patches (i.e. communities). While local food webs depict the possible pathways for energy propagation among

populations within the same community, landscape networks—that describe how species movements connect habitat patches—depict the possible pathways for energy spreading across habitats within a landscape (Urban & Keitt, 2001). The integration of both network types, where local food webs are entangled in landscape networks, forms spatially coupled meta-food webs that capture the transfer of energy in meta-communities (Figure 1, Ryser et al., 2021). The spatial interconnections of distinct local food webs, as well as the strength of these connections, are associated with mechanisms that can change the persistence of populations locally (Allhoff et al., 2015). For instance, some populations that would have gone extinct in a local community can persist because of the constant immigration of individuals from neighbouring habitat patches. This rescue effect (Brown & Kodric-Brown, 1977) can occur directly, when individuals of a given species support the local population of the same species (Brown & Kodric-Brown, 1977) or indirectly, when this inflow of individuals creates more favourable biotic conditions locally, for instance by increasing the amount of resources available (Ryser et al., 2019). Overall, any perturbation acting on one network will have consequences on the other one (Scotti et al., 2013). Therefore, the energetic integrity of a local community not only depends on species' ability to acquire and spread resources through trophic interactions within the local food web but also on how they are connected to other habitat patches and food webs within a landscape.

This spatially explicit view of ecological communities is currently being ignored by food web approaches aiming to identify important species in ecosystems, which questions our ability to derive sound conservation practices at the landscape level. Indeed, species with a high ability to spread energy within local food webs are not necessarily the ones that would spread energy across different habitat patches, which implies that what is considered an important species locally can differ from a real-world context where communities are spatially connected. The importance of energy circulation in meta-communities for species coexistence (Ryser et al., 2021) advocates for using methods explicitly integrating spatial coupling, such as global network approaches developed for food webs. We here extend the work of Allesina and Pascual (Allesina & Pascual, 2009)—who adapted the PageRank algorithm, commonly used to sort internet pages by importance, to food webs—to identify key species in a meta-community context. First, we present how species importance in food webs and patch importance in landscape networks can be estimated, separately, before developing the integration of these networks. We then use this framework to show that (1) species that are considered important in isolated communities are not necessarily the same as the ones considered important when the whole landscape is taken into account. Moreover, (2) the importance of a patch in the landscape network will affect the importance of the populations it hosts (important patches, e.g. central patches, tend to host important populations). To summarise, it means that the importance of a species is influenced by both intrinsic factors (dispersal capacity, trophic position) and extrinsic factors (the position of the patch in the landscape network).

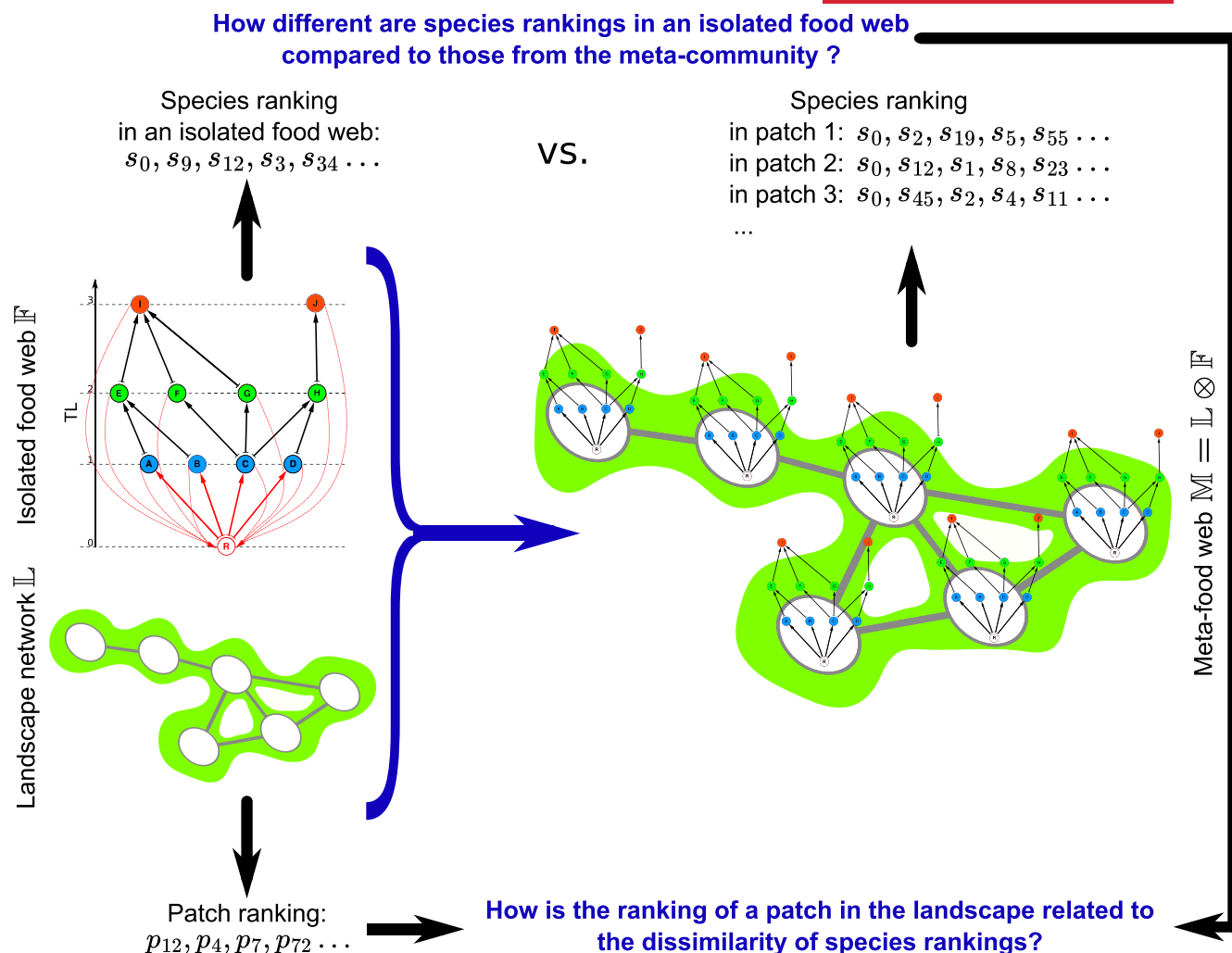


FIGURE 1 How do patch rankings in the landscape relate to the importance of local populations and to the dissimilarity of species rankings across patches? Conceptual representation of the workflow and of the integration of food webs into landscape networks.

2 | QUANTIFYING IMPORTANCE IN DIFFERENT TYPES OF NETWORKS

All variables and mathematical definitions are summarised in [Table S1](#). Associated code is available in Rollin (2024).

2.1 | PageRank and CheiRank algorithms for food web

The original PageRank algorithm (Brin & Page, 1998; Langville & Meyer, 2012) models a random walk on the World Wide Web (WWW) in order to assess the importance of internet pages. It mimics the journey of a web surfer that follows randomly the succession of hyperlinks leading to new web pages. In this case, the WWW is a complex network whose nodes are the web pages and the directed edges are the hyperlinks. This complex network can be represented by the adjacency matrix A in which the presence or absence of a link from page i to page j is defined by the matrix entry A_{ji} . The PageRank algorithm relies on a stochastic matrix S

that describes the probabilities of transition between nodes in the network, defined as

$$S_{ss'} = \frac{A_{ss'}}{k_{s'}^{\text{out}}}, \quad (1)$$

where $k_{s'}^{\text{out}}$ is the out-degree of node s' (i.e. the number of links out of node s'), and $A_{ss'}$ represents the adjacency matrix element, which is 1 if there is a link from s' to node s , and is 0 otherwise. This network approach allows for an analogy with food webs, for which the adjacency matrix represents the presence or absence of trophic interaction (the edges) between species (the nodes), (Gauzens et al., 2016). The use of networks permits better correspondences between the CheiRank algorithm, which can be seen as a quantification of how nutrients will distribute in the network. The PageRank algorithm can be applied to food webs to estimate species importance (Allesina & Pascual, 2009). However, to use the PageRank algorithm, the stochastic matrix S associated with the network has to be irreducible (i.e. no permutation of rows and columns allows transforming S into an upper triangular block matrix) and primitive (i.e. the leading eigenvalue of S is a positive real number strictly greater than the module of the others eigenvalues).

These two mathematical properties imply that the network is connected, that is there always exists a path connecting each pair of nodes, and that the stochastic process encoded by S leads to a unique steady state. This is not necessarily the case for food webs, because of their directed nature (energy flows from a resource to its consumer). Using the PageRank and the CheiRank algorithms is similar to sending a random surfer wandering forever in the food web as well as in the food web with inverted link directions, respectively. To allow the random surfer to probe the entire food web, we have to prevent it from being stuck in node sinks (for instance top species, which do not point toward other species) or in possible isolated sub-networks. A solution could have been to add a teleportation term to the stochastic matrix S , this solution is indeed retained in the case of the WWW (once the web surfer is bored, he can decide to no more follow web links on the page web and enter a new url). Here, we choose the solution from (Allesina & Pascual, 2009) to add a root node to which all other nodes point (see the red R node in the isolated food web in Figure 1 and Figure S2, in Supporting Information 2). This approach seems preferable in a food web context as it directly corresponds to an ecological process. The root nodes represent a nutrient pool for the associated community. The return to the root node mimics the unavoidable recycling of the species, and the root node acts as a resource pool for the basal species. In practice, we consider $n + 1$ species. To estimate node importance, we start by assuming an initial distribution $\mathbf{P}^{(0)} = (P_{s_0}^{(0)}, P_{s_1}^{(0)}, \dots, P_{s_n}^{(0)})^T$. The element $P_s^{(0)}$, where s stands for any of the $n_j + 1$ species, say $s_0, s_1, \dots, s_n$, gives the initial probability of the presence of a hypothetical random surfer on the node s . Hence, after the m th iteration of this surfer moving through the network links, the probability of ending up on the node s' is $P_{s'}^{(m)}$ given by $\mathbf{P}^{(m)} = S^m \mathbf{P}^{(0)}$. The steady state of such a stochastic process is characterised by the PageRank vector $\mathbf{P} = (P_{s_0}, P_{s_1}, \dots, P_{s_n})^T$ defined such as $S\mathbf{P} = \mathbf{P}$. Then, sorting species by descending order of the value of their PageRank probabilities, that is P_s for the species s , allows ranking of the species in accordance to their ability to catch nutrients from the rooted food web $\mathbb{F}$ (see Figure 1). For each species s we assign a PageRank index $k_s \in \{1, \dots, n_j + 1\}$ such as if $P_s > P_{s'}$, that is if the species s is a more efficient nutrient catcher than the species s' , then $k_s < k_{s'}$, and conversely. The species with a PageRank index equal to 1 is the most important species according to the PageRank algorithm, that is it is the most efficient nutrient catcher of the rooted food web $\mathbb{F}$, the species with a PageRank index equal to 2 is the second most important, and so on.

Following Allesina and Pascual (2009), we are interested in the relative importance of each species in terms of the support to other species, which can be obtained from the CheiRank vector $\mathbf{P}^*$ (Chepelianskii, 2010; Zhirov et al., 2010). Here, the elements of the corresponding stochastic matrix S^* are

$$S_{ss'}^* = \frac{A_{s's}}{k_{s'}^{\text{in}}}, \quad (2)$$

where $k_{s'}^{\text{in}} = \sum_{s \in \mathbb{F}} A_{s's}$ is the in-degree of the node s' , that is the number of prey of species s' . The above defined out-degree $k_{s'}^{\text{out}}$ of the node s' is then the number of predators of the species s' . Similarly to the PageRank algorithm, the steady state of the associated stochastic process is

characterised by the CheiRank vector $\mathbf{P}^* = (P_{s_0}^*, P_{s_1}^*, \dots, P_{s_n}^*)^T$ defined such as $S^* \mathbf{P}^* = \mathbf{P}^*$. Here, sorting the species by descending order of the value of their CheiRank probabilities, i.e. P_s^* for the species s , allows ranking the species in accordance to their ability to spread nutrients through the food web and support other species (Allesina & Pascual, 2009). In Allesina and Pascual (2009), Allesina and Pascual showed that this ranking gives a good extinction order to find the most efficient route to collapse a trophic network. For each species s we assign a CheiRank index $k_s^* \in \{1, \dots, n_j + 1\}$ such as if $P_s^* > P_{s'}^*$, that is if the species s is a more efficient nutrient spreader than the species s' , then $k_s^* < k_{s'}^*$, and conversely. The species with a CheiRank index equal to 1 is the most important species according to the CheiRank algorithm, that is the most efficient nutrient spreader, the species with a CheiRank index equal to 2 is the second most important, and so on.

2.2 | PageRank algorithm for the landscape network

The nodes of the landscape network $\mathbb{L}$ are the patches (or habitats) and the links are the paths between patches (see Figure 1). The number of patches is n . We assume that the path from a node to another one can be taken either way, so the links are bidirectional and the landscape network is non-directed. The associated stochastic matrix S has the elements

$$S_{pp'} = \frac{A_{pp'}}{k_{p'}}, \quad (3)$$

where $A_{pp'} = 1$ if there is a path between patches p and p' , and $A_{pp'} = 0$ otherwise. The quantity $k_{p'} = \sum_{p \in \mathbb{L}} A_{pp'}$ gives the number of patches which are connected to the patch p' . The stochastic matrix element $S_{pp'}$ gives the rate of transition from the patch p' to the patch p . We define then the PageRank vector $\mathbf{P} = (P_{p_1}, \dots, P_{p_n})$ as the steady-state of the corresponding stochastic process, $S\mathbf{P} = \mathbf{P}$. The value of P_p is proportional to the number of times a random walker, forever wandering inside the landscape network $\mathbb{L}$, hits the patch p . Similarly to the procedure followed previously in the Section 2.1, we assign a PageRank index K_p to each patch. The patch with $K_p = 1$ is the most central patch according to the PageRank algorithm, that is the most visited one, the one with $K_p = 2$ is the second most central, and so on. Otherwise stated, if $P_p > P_{p'}$ or equivalently $K_p < K_{p'}$, then the patch p is more often visited by a random walker than the patch p' .

We note that the non-directed nature of the landscape network $\mathbb{L}$ would give a CheiRank probability vector exactly the same as the above-defined PageRank probability vector since the inversion of the direction of the links leaves the landscape network $\mathbb{L}$ unchanged.

2.3 | CheiRank algorithm for the meta-food web

Each node of the meta-food web $\mathbb{M}$ is defined by a species s and a patch p . The elements of the adjacency matrix $\mathcal{A}$ associated to the meta-food web $\mathbb{M}$ are then

$$\mathcal{A}_{sp,s'p'} = \begin{cases} \mathcal{A}_{ss'} & \text{if } p=p', \\ w_{s,p \leftrightarrow p'} & \text{if } p' \neq p \text{ and } s'=s, \\ 0 & \text{if } p' \neq p \text{ and } s' \neq s. \end{cases} \quad (4)$$

As long as we consider the same patch, that is $p = p'$, the elements $\mathcal{A}_{sp,s'p'}$ of the meta-food web adjacency matrix $\mathcal{A}$ are the same as those of the cloned rooted food web $\mathbb{F}$, that is $\mathcal{A}_{sp,s'p'} = \mathcal{A}_{ss'}$. We assume that the same rooted food web $\mathbb{F}$ is duplicated on every patch. Once we consider different patches, that is $p \neq p'$, a non-zero value is possibly assigned to populations of the same species adjacency matrix element $\mathcal{A}_{sp,s'p'} = w_{s,p \leftrightarrow p'}$ if a link exists between patches p and p' , otherwise a zero value is assigned $\mathcal{A}_{sp,s'p'} = 0$. This representation allows coding for population-specific links in the landscape networks: not necessarily all populations from a patch can disperse to the neighbouring patches. Moreover, the non-binary approach permits using species-specific strengths for dispersion links.

We assumed that no trophic interactions take place during the dispersion process. This implies that the energy transfer from one patch p to another patch p' is always occurring between populations of the same species within both patches. Hence, $\mathcal{A}_{sp,s'p'} = 0$ if $s \neq s'$.

The inter-patch weight $w_{s,p \leftrightarrow p'}$ is a priori dependent both on the considered species s and on the distance $d_{p \leftrightarrow p'}$ between the patches p and p' . It can be considered as the transition probability of a species s to cover the distance between two patches p and p' .

The CheiRank vector $\mathcal{P}^*$ of the meta-food web $\mathbb{M}$ is obtained from the stochastic matrix $\mathcal{S}^*$ which the elements are

$$\mathcal{S}_{sp,s'p'}^* = \frac{\mathcal{A}_{s'p',sp}}{k_{s'}^{\text{in}} + w_{s'p'}}, \quad (5)$$

where $k_{s'}^{\text{in}}$ is the number of prey of the species s' in the cloned rooted food web $\mathbb{F}$ and $w_{s'p'} = \sum_{p \in \mathbb{M}} w_{s',p \leftrightarrow p'}$ is the sum of the transit probabilities of the population of species s' living in any patch p of the landscape network $\mathbb{L}$ toward the patch p' .

As expected, the matrix $\mathcal{S}^*$ stochastic property is ensured as we have $\sum_{(sp) \in \mathbb{M}} \mathcal{S}_{sp,s'p'}^* = 1$. The CheiRank vector $\mathcal{P}^*$ is defined such as $\mathcal{S}^* \mathcal{P}^* = \mathcal{P}^*$. The CheiRank probability $\mathcal{P}_{sp}^*$ measures the ability of the population of species s living in the patch p to sustain all the other populations living in all the patches of the meta-food web $\mathbb{M}$. The average CheiRank probability of the species s over the whole meta-food web is $\mathcal{P}_s^* = \sum_p \mathcal{P}_{sp}^*$, it measures the average ability of the species s to support the different local populations over the whole meta-food web $\mathbb{M}$. The quantity $\mathcal{P}_p^* = \sum_s \mathcal{P}_{sp}^*$ measures the ability of the patch p to sustain the entangled trophic network constituted by the meta-food web $\mathbb{M}$.

As in the cases of the food web $\mathbb{F}$ or of the landscape network $\mathbb{L}$, it is possible to establish a ranking list $\{K_{s_0 p_1}^*, \dots, K_{s_{n_1} p_1}^*, K_{s_0 p_2}^*, \dots, K_{s_{n_1} p_2}^*, \dots, K_{s_0 p_{n_p}}^*, \dots, K_{s_{n_1} p_{n_p}}^*\}$, such as, if $K_{sp}^* < K_{s'p'}^*$, or equivalently $\mathcal{P}_{sp}^* > \mathcal{P}_{s'p'}^*$, the species s in the patch p better supports the meta-community than the species s' in the patch p' .

3 | SPECIES IMPORTANCE FROM LOCAL FOOD WEBS TO META-COMMUNITIES, INSIGHT FROM SYNTHETIC NETWORKS

3.1 | Methods

3.1.1 | Generation of the data

We generate random food webs with $n = 30$ species using the niche model (Williams & Martinez, 2000) with a connectance close to $C = n/n_j^2 = 0.1$. We chose to use the niche model as it relies on very few ecological assumptions, offering a good compromise between model complexity and ecological realism (Allesina et al., 2008), favouring the generality of our results. Here, n is the number of trophic links in the food web. Figure S1 describes the transformation of a food web into the corresponding rooted food web $\mathbb{F}$. Following (Johnson et al., 2014; Levine, 1980), the trophic level TL_s of the species s is defined as 1 plus the average trophic level of its prey (the trophic level of basal species is set to 1). We associate a body mass m_s to species s depending on its trophic level TL_s . The theoretical law giving the mass m_s of the species s according to its trophic level is $m_s/m_0 = R^{TL_s-1+\xi}$ where m_0 is the characteristic mass of the first trophic level, R is the average body-mass ratio between two species whose trophic levels differ by one unit, here we take $R = 100$, and ξ is a random variable sampled from a normal distribution with a mean of 0 and a standard deviation of 0.1.

The landscape network $\mathbb{L}$ is a random geometric graph with $n = 100$ nodes. These nodes correspond to the patches of the landscape. The n patches are then randomly and homogeneously distributed in the unit square. This random approach was chosen to minimise the hypotheses to use and derive some very general principles from our results. Two patches p and p' are connected if they are separated by an Euclidean distance $d_{p \leftrightarrow p'} < r$. Here, we take the threshold value $r = 0.2$ to ensure a moderate degree of connectivity between the different patches, preventing species from dispersing to too many nodes and preventing the occurrence of disconnected (i.e. isolated) patches. The landscape graph is non-directed and species populations can transit between patches with no privileged direction. The connected and non-directed nature of the landscape network ensures that there is no isolated patch (or group of patches) that would prevent the calculation of Page and CheiRank indices as described in Section 2.2. In the following, a weight will be assigned to each link of the landscape network depending on the ability of a species to travel the corresponding distance between two patches.

We generate a meta-food web $\mathbb{M}$ by replicating the same rooted food web $\mathbb{F}$ in all the different landscape patches of the network $\mathbb{L}$. We used three different scenarios to determine how species can disperse from one patch to another one and, consequently, to assign a weight $w_{s,p \leftrightarrow p'}$ to inter-patch links. In the first scenario, all species can disperse between two patches as soon as they are connected in the landscape network $\mathbb{L}$. The second and third scenarios introduce a dispersion distance threshold that is species-specific, and based on their body mass. More precisely:

- Type 1: All species are able to disperse between two patches as soon as they are connected in the landscape network. The inter-patch weight is species independent: $w_{s,p \leftrightarrow p'} = w$ for all the species. For this type of inter-patch weight, we consider the values $w = 0.0001$ corresponding to the regime where the duplicated food webs and the landscape network are almost totally decoupled (the nutrients are preferentially exchanged inside each patch and rarely travel from a patch to another), $w = 0.1$ corresponding to a moderate coupling, and $w = 1$ corresponding to a strong coupling for which the inter-patch weights are equal to the trophic links weights of the food web (the nutrients travel either across the food web or the landscape network).
- Type 2: a species dependent weight $w_{s,p \leftrightarrow p'}$ which is equal to 1 if the species distance threshold d_s is greater than the inter-patch distance $d_{p \leftrightarrow p'}$ and equal to 0 otherwise,
- Type 3: the species dependent weight $w_{s,p \leftrightarrow p'}$ defined in Equation (6) taking values inside the range $[0, 1]$ depending on the distance $d_{p \leftrightarrow p'}$ between the two patches and on the species distance threshold d_s .

Assuming that the biggest species, that is the one with a mass $m_{\max} = \max_{s \in \mathbb{F}} \{m_s\}$, is able to reach a maximal distance of r , the normalised distance reachable by the species s is $d_s = r(m_s/m_{\max})^\beta$, where $\beta = 0.05$ is the body mass scaling exponent. Hence, for the species s , the probability of transit $w_{s,p \leftrightarrow p'}$ from the patch p to the patch p' , and vice versa, is assumed to follow a linear decrease with the actual distance $d_{p \leftrightarrow p'}$ between the two patches

$$w_{s,p \leftrightarrow p'} = \begin{cases} \max\left(0, 1 - \frac{d_{p \leftrightarrow p'}}{d_s}\right) & \text{if } p \leftrightarrow p', \\ 0 & \text{if } p \not\leftrightarrow p'. \end{cases} \quad (6)$$

The first line in Equation (6) concerns the case where a path actually exists between patches p and p' . If the maximum distance reachable by the species s is less than the distance between the patches p and p' , that is $d_s \leq d_{p \leftrightarrow p'}$, then the transition rate is zero, $w_{s,p \leftrightarrow p'} = 0$. In the opposite case, this rate $w_{s,p \leftrightarrow p'} = 1 - d_{p \leftrightarrow p'} / d_s$ decreases linearly with the inter-patch distance $d_{p \leftrightarrow p'}$. The second line in Equation (6) concerns the case when there is no geographical path between patches p and p' .

Mathematically, the meta-food web $\mathbb{M} = \mathbb{L} \otimes \mathbb{F}$, as depicted in Figure 1a, is the tensor product of two networks, the landscape network $\mathbb{L}$ and the rooted food web $\mathbb{F}$. Hereafter, we will consider hundreds of randomly generated meta-food webs with $(n + 1) \times n = 3100$ nodes.

To assess how the position of a food web in the landscape network affects the importance of species locally, we examined how species' CheiRank values change with the rank of patches from the landscape network.

3.1.2 | Dissimilarity of the food webs

We here compare the ranking of the species in the isolated food web $\mathbb{F}$ with the relative ranking of its population inside a given

patch p of the landscape $\mathbb{L}$. For this purpose, we use the Kendall distance allowing to compare the differences between two ordered lists (in our case, two possible species rankings). Let us consider the n species to which we assign the labels $\{s_1, \dots, s_n\}$. As introduced in Section 2.1, the CheiRank algorithm allows to rank the species populations of the isolated food web $\mathbb{F}$ according to their relative ability to support other populations in the isolated food web: we obtain the CheiRank list $k^* = \{k_{s_1}^*, \dots, k_{s_n}^*\}$. As introduced in Section 2.3, the CheiRank algorithm allows ranking all pairs species-patch (s, p) of the meta-food web $\mathbb{M}$. Focusing on a given patch p , we obtain the CheiRank list $k_p^* = \{K_{s_1,p}^*, \dots, K_{s_n,p}^*\}$. The Kendall distance (Cicirello, 2020) between the CheiRank list k^* of the species populations in the isolated food web $\mathbb{F}$ and the CheiRank list k_p^* of the same species populations but living in the patch p of the meta-food web $\mathbb{M}$ can be defined as

$$d_{k^*, k_p^*} = (1 / (n_s(n_s - 1))) \sum_{(s, s')} \left[1 - \text{sign}(k_s^* - k_{s'}^*) \text{sign}(K_{s,p}^* - K_{s',p}^*) \right], \quad (7)$$

where the sum runs over all the different pairs (s, s') of species, and the function $\text{sign}(x) = x / |x|$ gives the sign of x , either $+1$ or -1 . The Kendall distance d_{k^*, k_p^*} takes values from 0, for two lists k^* and k_p^* representing the same ordering of the n species, to 1, for two lists where one represents the exact reverse ordering of the other, and conversely. The metric defined by Equation (7) counts the number of pairwise disagreements between the two ranking lists k^* and k_p^* .

3.2 | Results

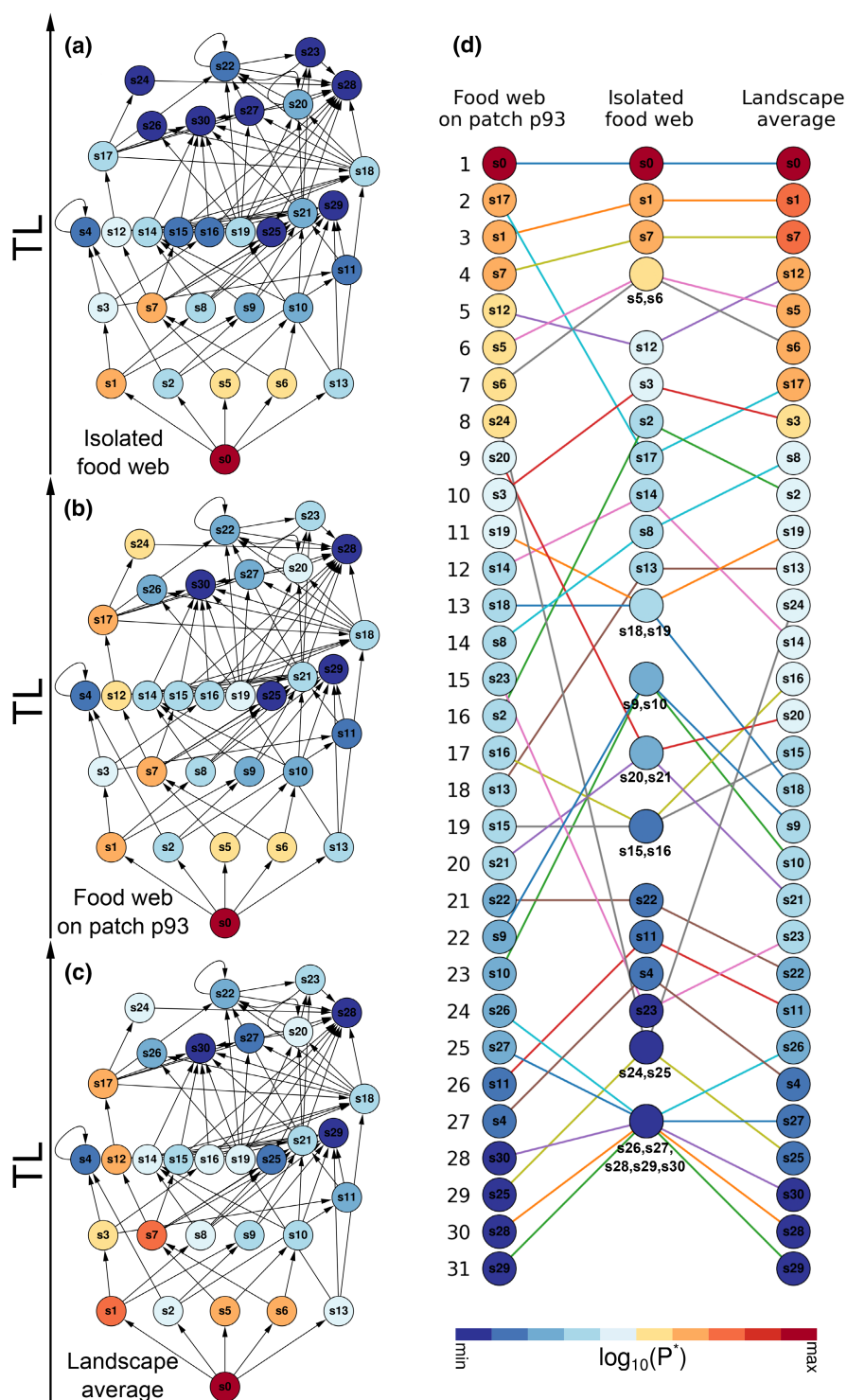
3.2.1 | Isolated food web versus meta-food web CheiRank analysis for an example food web

We present an illustration of how the importance of a species can change depending on the spatial context using an example of a rooted food web $\mathbb{F}$ (Figure 2a).

Trivially, the root node s_0 has by far the highest CheiRank probability of all food webs, the isolated one (Figure 2a), but also all food webs in the meta-community context (Figure 2b,c). This is obvious since it supports the entire food web and its removal would mechanically lead to the extinction of all the other species. Then, species considered as important tend to be located at the lower part of the isolated rooted food web $\mathbb{F}$ (Figure 2a) but with important differences within trophic levels (e.g. basal species s_1, s_5, s_6, s_7 from the isolated food web have CheiRank probabilities greater than the ones of species at higher trophic levels). Indeed, according to the CheiRank algorithm, the more a species supports important supporting species, the more it is an important supporting species (recurrence definition).

We duplicate now the rooted food web $\mathbb{F}$ into each patch of the landscape network $\mathbb{L}$ in order to construct the meta-food web $\mathbb{M}$. We use a dispersal that is dependent on species body mass, as above defined in the type 3 scenario (6). We begin by outlining the differences in CheiRank distributions between the isolated food web $\mathbb{F}$

FIGURE 2 Typical food webs coloured according to the CheiRank probabilities. The species s node is coloured from dark blue (min) to dark red (max) according to its: (a) CheiRank probability value P_s^* of the species in the isolated rooted food web $\mathbb{F}$, (b) CheiRank probability value $P_{s,p_{93}}^*$ of the species in the patch p_{93} harbouring the most dissimilar rooted food web to the isolated rooted food web $\mathbb{F}$, (c) CheiRank probability value P_s^* averaged over all the patches of the landscape network $\mathbb{L}$. The minimum and the maximum values of the CheiRank probabilities are: (a) $\min_s(\log_{10} P_s^*) \simeq -2.08$ and $\max_s(\log_{10} P_s^*) \simeq -0.61$, (b) $\min_s(\log_{10} (P_{s,p_{93}}^* / P_{p_{93}}^*)) \simeq -2.15$ and $\max_s(\log_{10} (P_{s,p_{93}}^* / P_{p_{93}}^*)) \simeq -0.71$, (c) $\min_s(\log_{10} P_s^*) \simeq -2.21$ and $\max_s(\log_{10} P_s^*) \simeq -0.79$. For the sake of visibility, the recycling links “species $\rightarrow$ root” are not shown (as an example, see red coloured dotted links of isolated food web $\mathbb{F}$ in Figure 1). The panel (d) shows the ranking of the species: (middle column) living in the isolated food web $\mathbb{F}$, (left column) living on the patch p_{93} , (right column) averaged over all the patches of the landscape network $\mathbb{L}$. For the isolated food web, the corresponding minimum rank is assigned to tied species.



(Figure 2a) and its counterpart in the meta-community context which exhibits less similarity to it (Figure 2b, the most dissimilar patch being here p_{93}). In a second step, we compare the CheiRank distributions of the isolated rooted food web to an averaged CheiRank distribution across all patches (Figure 2c).

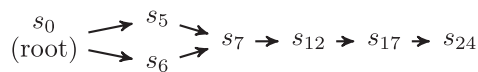
We observe, within the patch p_{93} (Figure 2b), that the species with the highest CheiRank probabilities are less systematically located at the bottom of the sub-network (species with low TL). This difference with the isolated food web $\mathbb{F}$ (Figure 2a) is due to possible

displacements of species through the whole landscape $\mathbb{L}$. From the species ranking (Figure 2d), we observe that species s_{17} , with rank 9 in the isolated food web, is the most important species in the patch p_{93} , with rank 2 (the non-living root node has the rank 1). Also species s_{24} gains 17 places since it passes from rank 25 in the isolated food web to rank 8 in patch p_{93} . Additional species obtain a significantly better ranking in patch p_{93} (e.g. species s_{20} and s_{23}) whereas others obtain a significantly lower ranking (e.g. TL = 1 species s_3 and s_{13} which passes from rank 7 to 10 and from rank 12 to 18, respectively). Hence, from

one patch to another, the relative ability of a species to support the others can substantially change.

Also, from Figure 2d, we observe that the existing ties in the isolated food web $\mathbb{F}$ ranking are removed due to the different species displacement capabilities over the landscape $\mathbb{L}$ (e.g. the species s_5 and s_6 , which are equivalent for the CheiRank algorithm as they both provide food for species s_7 and s_{10} , have the same ranking in the isolated food web and different rankings in the patch p_{93}).

To obtain the average CheiRank probability distribution $\mathcal{P}_s^*$ for the meta-community in Figure 2c we summed the CheiRank probabilities $\mathcal{P}_{sp}^*$ over all the patches (see Section 2.3). The obtained space averaged CheiRank probability distribution clearly exhibits differences with the isolated rooted food web $\mathbb{F}$ (Figure 2a). In particular, we observe a preferential food path



which, on average, sustains the whole meta-food web $\mathbb{M}$ (and that is also visible on p_{93}). In addition, some top predators, that is s_{20} , s_{23} and s_{24} , have a better averaged CheiRank probability in the meta-food web $\mathbb{M}$ (see Figure 2c) than in the isolated rooted food web $\mathbb{F}$ (see Figure 2a). These top predators are therefore critical to sustaining the meta-food web, and considering them only in isolated food webs tends to underestimate this importance. Particularly, from Figure 2d (right column), although the species s_{24} (rank 13) is a top predator with $TL > 4$ (see Figure 2a), it plays a non-negligible role in maintaining the energetic integrity of the meta-community.

3.2.2 | Statistical analysis of the dissimilarity between an isolated food web and the meta-food web

In the following, we assess how this consideration of the landscape network alters our definition of important species. As before, we consider a meta-food web $\mathbb{M}$ constituted by an underlying landscape $\mathbb{L}$ of patches hosting in each patch the same rooted food web $\mathbb{F}$. However, we use two replicated approaches to explore how variability in food web or landscape structures might affect our results. First, we kept the landscape network constant and varied the food web structure. We created 100 meta-food webs $\mathbb{M}$ that differ by the rooted food web used (100 different food webs were generated and combined with the same landscape network). Second, we kept the food web structure constant and varied the landscape network. We created 100 meta-food webs $\mathbb{M}$ that differ by the landscape network used (100 different landscape networks were generated and combined with the same food web). For both approaches, we consider the three different types of inter-patch weights $w_{s,p \rightarrow p'}$ ensuring the diffusion of populations from patch to patch over the landscape: (1) independent of species, (2) different links depending on species body mass, same weight for all species and (3) species-specific link and link weight (see Section 3.1.1 for a detailed description). For each generated meta-food web, we compute the CheiRank vector

and we rank all the species living in the landscape according to their CheiRank probability.

For a given meta-food web $\mathbb{M}$, we compute the Kendall distances d_{k^*,k_p} (7) between the CheiRank list of the species belonging to the isolated food web $\mathbb{F}$ and the CheiRank list of the species living inside each patch of the landscape hosting all the same food web $\mathbb{F}$. In Figure 3, we present the results obtained for our two approaches.

The panel Figure 3a shows for each patch p the average $\overline{d_{k^*,k_p}}$ of the Kendall distance over the 100 random realisations of the meta-food web and for the species-independent inter-patch weights (type 1). In abscissa, the landscape patches are ordered according to their respective PageRank index K_p obtained from the PageRank vector associated with the landscape network $\mathbb{L}$. As expected, the almost decoupled regime $w = 0.0001$ (blue points in Figure 3a) leads to a Kendall distance close to 0 for all the patches. For the moderate coupling regime $w = 0.1$ (green points in Figure 3a), the distance $\overline{d_{k^*,k_p}}$ globally drops as the landscape PageRank index K_p of the patch increases. Indeed, we expect that the populations living on the most (less) central patches are the most (or less) impacted by the structure of the underlying landscape network. In the strong coupling regime $w = 1$ (red points in Figure 3a), the drop is less pronounced. In this regime, the weights of the food web links and the inter-patch weights are equal. Consequently, we can consider that the duplicated food webs and the landscape network are merged into a single network. Otherwise stated, nutrients can pass as easily from one species to another as from one patch to another.

The panel Figure 3b presents the average Kendall distance $\overline{d_{k^*,k_p}}$ for the species dependent inter-patch weights (types 2 and 3). These types of species diffusion are by far more realistic as they take account of the body mass-dependent ability of each species s to travel over a given distance (i.e. the distance threshold d_s is body mass-specific). Globally, as observed in Figure 3a for the species-independent type of inter-patch weights, the curves follow the same trend, that is the food webs located on the most central patches of the landscape have the largest Kendall distance from the isolated food web, and conversely, the less central ones have the smallest distance. But, more interestingly, the drop of the Kendall distance with the landscape PageRank centrality of the patches is only a trend as the drop is no more monotonous and non-negligible fluctuations of the mean now appear: two patches with comparable PageRank indices K_p may exhibit an up to 0.1 difference of degrees of dissimilarity with the isolated rooted food web. The fluctuations are more pronounced for the type 2 species diffusion (magenta points) than for the type 3 species diffusion (orange points) which is more realistic. Indeed, even not very central patches in the landscape according to the PageRank algorithm harbour food webs with the maximum dissimilarity with the isolated rooted food web. The top PageRank patches are not necessarily the most dissimilar ones with the isolated food web; this is particularly true for the type 2 species mobility model. For this type 2 mobility model, we can see that the distribution of species importance in the rooted food webs from patches with PageRank indices 75 and 76 are the ones that differ the most from the isolated food web. For the type 3 mobility scenario, the strongest difference is observed for the patch with a PageRank index of 36. Interestingly, the results obtained with our second approach,

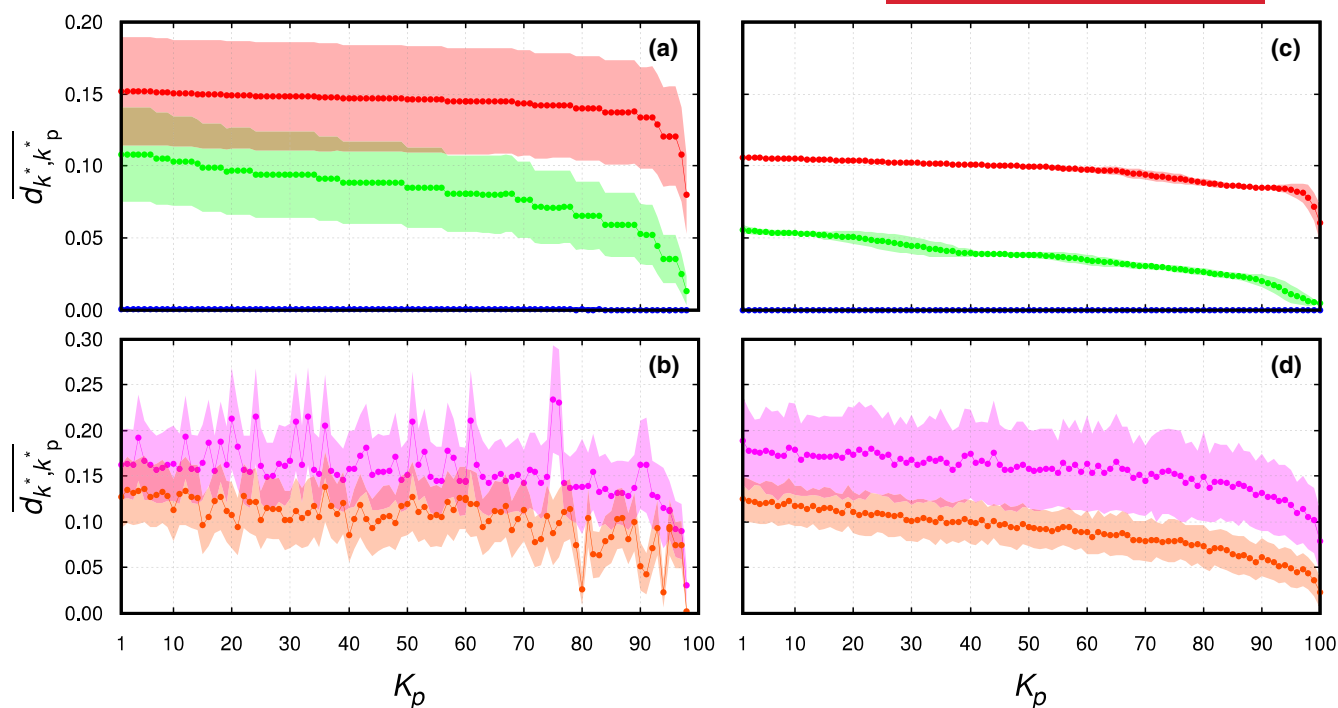


FIGURE 3 Dissimilarity between the food webs located on the patches and the isolated food web. The Kendall distance d_{k^*, k_p} is computed between the CheiRank list of species in the isolated rooted food web F and the CheiRank list of species in the food web located on a given patch of the meta-food web M . In (a) and (b), the average $\overline{d_{k^*, k_p}}$ is done over 100 randomly generated meta-food webs keeping the same underlying landscape network and randomly generating new cloned rooted food web F . In (c) and (d), the average $\overline{d_{k^*, k_p}}$ is done over 100 randomly generated landscape networks keeping the same food web. Along the abscissa, the patches are ordered by their PageRank indices K computed from the non-directed landscape network L . Panels (a) and (c) present the computed distances for the type 1 species independent inter-patch weights with $w = 0.0001$ (blue), $w = 0.01$ (green), and $w = 1$ (red). The minimum, the mean, the standard deviation, and the maximum of the averaged Kendall distance $\overline{d_{k^*, k_p}}$ are 0.0001, 0.0004, 0.0001, 0.0005 for $w = 0.0001$, 0.0134, 0.0817, 0.0196, 0.1079 for $w = 0.01$, and 0.0801, 0.1437, 0.01, 0.1520 for $w = 1$. Panels (b) and (d) present the computed distances for the species-dependent inter-patch weights, type 2 (magenta) and type 3 (orange). The minimum, the mean, the standard deviation, and the maximum of the averaged Kendall distance $\overline{d_{k^*, k_p}}$ are 0.0305, 0.1569, 0.0284, 0.2346 for type 2 and 0.0025, 0.1045, 0.0243, 0.1383 for type 3. The shaded areas surrounding the different points delimit the $\pm \sigma$ standard deviation range associated with the random networks distribution.

applying variation on the landscape networks, are consistent with what we observed for the first approach. We observe a lower uncertainty around our central tendencies, as well as less patch-to-patch variability for types 2 and type 3 inter-patch weights (panel d). Importantly here, we calculated the PageRank of the different patches of the landscape network using the dispersal capacities of the largest species. However, for these type 2 and 3 mobility scenarios, the landscape network itself is species-dependent (the connection between the patches will differ between species). To assess whether our conclusion would hold when integrating this complexity, we estimated species-specific PageRank values for patches of a landscape network. We defined the PageRank value of a given patch as the average PageRank value we obtained using all species-specific landscape networks and reran our analysis of dissimilarity (as in Figure 3b). The results we obtained are qualitatively very similar to what we obtained when considering the landscape network associated with the largest species only. The full description of the adaptation made to the calculation of patch PageRanks and results are given in Supporting Information 3.

The most important feature is, independently of the species mobility model, that the food web's CheiRank can present on average

up to 15% differences with the isolated food web if we consider its environment and the possibility for species to travel throughout the landscape. Based on these results, we ran a subsequent analysis to assess how the position of a food web in the landscape network affects the importance of species locally. Using the same procedure as described before, we generated 100 different landscape networks (for which nodes were linked using the type 3 scenario), each associated with 100 different food webs. We observe (Figure 4) a decrease in species importance depending on their position on the landscape networks. This result therefore indicates that the most important species in meta-communities will mostly be observed in landscape patches considered as important.

4 | SPECIES IMPORTANCE FROM LOCAL FOOD WEBS TO META-COMMUNITIES: THE CASE OF THE BARENTS SEA

We tested the applicability of the algorithms and conducted the simulations on an empirical meta food web and local food webs

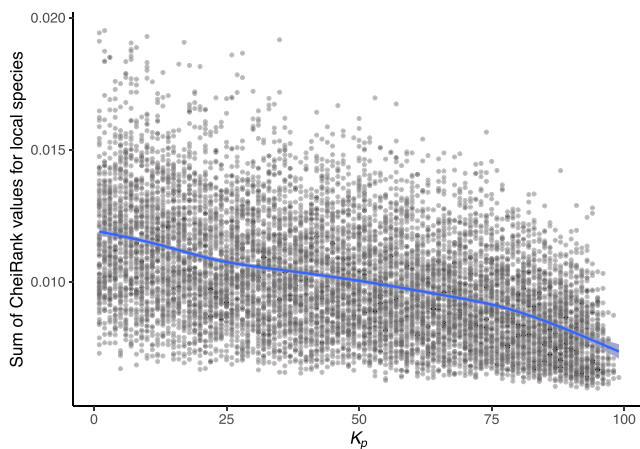


FIGURE 4 Effect of patch importance K_p on local species CheiRank values. Each dot represents the sum of CheiRank values of species on a patch of a landscape network, averaged over 100 different food webs. The blue line represents predictions from a GAM model using patch rank as a predictor variable. The blue shaded area represents the 95% confidence interval on model predictions.

using the Barents Sea—a high-latitude marine ecosystem—as a case study (Kortsch et al., 2019; Pecuchet et al., 2020a). The Barents Sea is characterised by a biogeographic divide with Atlantic species in the southwest and Arctic species in the north/northeast, as such it is a good ecosystem to test patterns of species dispersal between a metaweb and its local realisations. The meta-web encompasses the most common taxa in the Barents Sea from the seafloor to the surface, comprising 239 trophospecies and 2461 feeding interactions (Kortsch et al., 2018; Pecuchet et al., 2020b). The local food webs consist of 25 subregions within the Barents Sea (Kortsch et al., 2018). The boundaries of the subregions are to a large degree defined by the topography and enclose relatively homogenous areas with respect to hydrography and bathymetry (Hansen et al., 2016), two features known to influence species' distribution and dispersal in the Barents Sea.

The spatial dispersal links were based on species traits (Pecuchet et al., 2020b), and their spatial distribution and presence in the local food webs (Kortsch et al., 2018). Species can only disperse to local food webs in which they are present, for example polar bears are only present in the most Arctic sub-webs and therefore can only disperse within these, although they, as a species, are highly mobile. As a first approximation, we grouped species into three dispersal groups: group 1, sessile and slow species (mostly planktonic and benthic species, but can also be Arctic or bottom-dwelling fish); group 2, species of intermediate size and/or motility level (mostly benthic-pelagic and pelagic fish); group 3, motile and bigger species (seabirds, marine mammals, large motile fish and megabenthos). Species from group 1 can disperse into adjacent subregions, species from group 2 into the neighbours of the adjacent subregions, and species from group 3 can disperse into the three closest subregions to its own, which for the most highly motile and spatially distributed species results in almost all subregions. We did not weigh the dispersal links according

to the distance between patches (subregions). Therefore, we defined dispersion similarly to the type 2 scenario. We limited the definition of species dispersal group to three, but it is possible to define more, or other, groups based on species-specific traits such as body mass or locomotion mode.

In Figure 5, we see that the obtained dissimilarities between the local food webs and their isolated counterparts are higher in the empirical food webs compared to the synthetic counterparts (between 0.25–0.30 vs. 0.10–0.15). This suggests that our theoretical results might underestimate the differences in species importance occurring in real landscapes, likely due the way the food web and spatial meta-community networks were constructed in the theoretical example by using species body size as the only trait determining species interactions as well as dispersal capacity. In the empirical example, the trophic links within the different networks were mainly assigned using empirical observations (e.g. gut content analyses) and the presence of taxa within a subregion was based on field sampling or expert knowledge, integrating the effects of multiple species characteristics in structuring food webs and dispersal characteristics. Therefore, species' dispersal capacities and trophic levels are expected to be less correlated in this empirical example, leading to a less systematic effect of landscape connections.

5 | DISCUSSION

By proposing a method to estimate species' importance in meta-food webs, we were able to draw two main conclusions. First, species importance between the isolated food web and the different spatially connected food webs in the community changes depending on our dispersion scenario (i.e. all species have the same dispersion abilities vs. species-dependent abilities). When considering more realistic dispersion models for species (species-dependent inter-patch weights), fluctuations of dissimilarity no longer follow a monotonic pattern. As the model used here only relates to the topology of the two networks—the food web and the landscape network—this fluctuation is a signature of the entanglement of the food webs and the underlying landscape network through the body-mass-dependent species mobility. This means that the importance of a species population locally will relate to both its position in the food web (Allesina & Pascual, 2009; Jordán, 2009) and its capacity to move across patches in a landscape. Given the recent advocacy of functional trait approaches for identifying key species in ecosystems (Brun et al., 2022; Schleuning et al., 2023), our findings underscore the significance of encompassing not only traits associated with the roles and trophic positions of species within their communities but also traits linked to dispersion.

Second, we show the importance of considering the local context and the positioning of communities within their global environment when identifying important species. Indeed, we found substantial variation of species importance, both between food webs located in different patches of a meta-food web and between isolated food webs and food webs embedded in space. Overall, food webs from

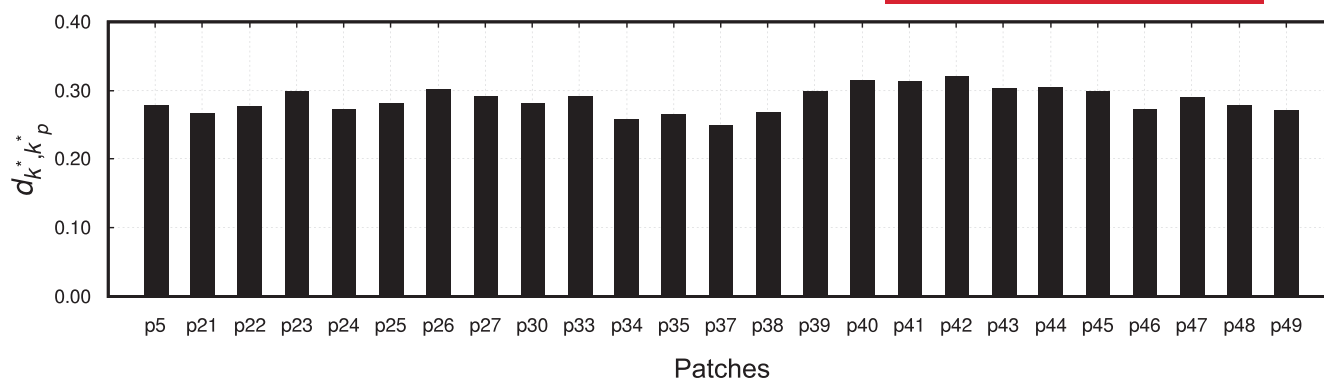


FIGURE 5 Empirical example of dissimilarity between food webs in metacommunities and isolated food webs. The Kendall distance d_{k,k_p} is computed between the CheiRank list of species in the isolated rooted food web $\mathbb{F}$ and the CheiRank list of species in the food web located on a given patch of the meta-food web $\mathbb{M}$.

central patches are the ones that differ the most from the isolated food webs, meaning that what are the important species in these central patches can be difficult to predict from the isolated network. As we observed that species from these central patches tend to be the most important in meta-communities, our results stress the need for a global consideration of space in the identification of important species. This context dependency of species importance leads to a fundamental conclusion: species importance is not necessarily the species characteristics associated with its identity, but a property that varies depending on the ecological context: a species considered as the most important in a patch of the landscape network might not be in another patch. On the whole, it means that the importance of a species is influenced by both intrinsic factors (dispersal capacity, trophic position) and extrinsic factors (position of the patch in the landscape network).

For the sake of completeness, we have also computed the dissimilarity in terms of the PageRank centrality instead of the CheiRank centrality (Section S4). While the CheiRank centrality quantifies the ability of species to distribute energy in the food web or the meta-community the PageRank centrality quantifies its ability to catch energy. The above conclusions drawn for the CheiRank centrality (see Figure 3a,b) hold also for the PageRank centrality (see Figure S3). Consequently, on average, the patches which capture nutrients the most efficiently are also the ones disseminating the most. These patches therefore act as energetic hubs in the spatially connected meta-food web. We note that such a combined CheiRank-PageRank analysis has been already applied to various directed networks such as the international trade network (see e.g. Coquidé et al., 2020), protein-protein interaction networks (see e.g. Lages et al., 2018), WWW-like networks (see e.g. Rollin et al., 2019; Zhironov et al., 2010), and causal ecological networks (Frossard et al., 2018). We leave such study of meta-food webs with underlying directed landscape networks for a further paper.

Although each duplicated food web is directed, the non-directed nature of the underlying landscape network dominates the meta-food web. It would be interesting to investigate the case of a directed landscape network modelling possible one-way inter-patch paths,

dead ends, or even asymmetric access to some habitat (for instance because of relief in mountainous areas). We argue that in this case, the combined CheiRank-PageRank analysis of the corresponding meta-food web will permit to better integrate habitat characteristics into model's predictions. Spatial links could for instance be parametrised based on the energy cost of dispersion (Berti et al., 2022) to further integrate habitat complexity as well as ecological and physiological processes.

Nowadays, the scientific community stresses the need to protect native and endangered biodiversity and preserve ecosystems, by among other restoring or preserving habitat connectivity (Cushman et al., 2013) and giving special care to important species (Valls et al., 2015). Our model is a first attempt to bridge these two approaches by potentially allowing the identification of which species in which patches are the most important to preserve to maintain the integrity of energy transfer at the landscape level. In empirical metacommunities, the occurrence of species in patches is strongly driven by the flux of individuals of different species moving from one patch to another, represented in our method by the fluxes of nutrients across the different links. However, while source-sink dynamics tend to support the persistence of species over time, extinction-recolonisation dynamics can also occur, leading to different species compositions in habitat patches over time. The method we propose here, however, is based on a snapshot of the community that ignores these temporal fluctuations in species occurrence. It therefore identifies the important species in the metacommunity based on the information available at a given point in time, and adding this temporal component is an interesting perspective to complement our approach. Multilayer networks (Pilosof et al., 2017) are suitable tools to formalise datasets compiling interaction networks at different points in time and model temporal interdependencies that can be analysed according to our methodology.

While we must acknowledge that current applications are yet limited by the amount of information needed to build meta-networks, the use of species functional traits offers some promising results. Body mass is a fundamental trait currently utilised with success to predict the distribution of trophic interactions among species (Gravel et al., 2013), as well as being allometrically coupled

to movement mode (e.g. crawling, flying, swimming, etc.) (Hirt et al., 2018). However, our empirical example—where the species functional traits used to determine trophic interactions and dispersal links differed—suggests that a finer description of links in the landscape and trophic networks could be decisive in determining species and population importance in meta-communities. As such, the predictive power of our theoretical model could further be enhanced by incorporating additional species traits such as movement mode, metabolic type, and foraging behaviour (Li et al., 2023). Lastly, species occurrence in the different patches can be estimated with models based on habitat suitability (Elith & Leathwick, 2009). The integration of multiple species traits, in opposition to our synthetic approach for building networks relying on body mass only could further increase the differences of importance between species in isolated food webs versus what would be observed in a metacommunity context (Figure 5). As such, the method we present has a strong potential for synergies with the recent development of functional trait approaches for conservation ecology (Gallagher et al., 2021).

AUTHOR CONTRIBUTIONS

Guillaume Rollin, José Lages and Benoit Gauzens conceptualised the study. Guillaume Rollin and José Lages made the methodological developments. Susanne Kortsch provided the empirical food webs for model validation. All authors contributed to the writing of the first draft of the manuscript, as well as to its review and edition. Guillaume Rollin developed the code used in this study.

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CONFLICT OF INTEREST STATEMENT

All authors declare that they have no conflicts of interest.

PEER REVIEW

The peer review history for this article is available at <https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/2041-210X.14384>.

DATA AVAILABILITY STATEMENT

The code underlying this study is available with a DOI at: <https://doi.org/10.5281/zenodo.11567641> (Rollin, 2024).

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SUPPORTING INFORMATION

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

Appendix S1: Mathematical definitions.

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