Social and landscape effects on food webs: a multi-level network simulation model

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One source of complexity in ecological systems is the hierarchical organization of parallel biological processes. Our ‘horizontal’ knowledge describing different levels is quite massive, but the understanding of their vertical interactions is very poor. We present a toy model linking social networks, food webs and a landscape graph. Horizontal processes refer to population, community and metacommunity dynamics, while vertical processes connect the three organizational levels. The model is stochastic and individual-based. We parametrized it by using reasonable empirical values found in the literature. Sensitivity analysis shows how the parameters describing the dynamics of a particular species (e.g., probability of social tie formation with conspecific individuals, or migration rate) can affect metapopulation size and spatial heterogeneity of all food web species. Changing the values of various parameters at any of the three levels have commensurable effects on the population size of all species. In contrast to the general intuition, community dynamics do not dominate population biology; social and landscape processes can trigger greater effects than food web interactions. More rapidly changing social relationships lead to a decrease in social network cohesion, thus impairing the feeding efficiency of consumers. In food webs, trophic specialization provides an advantage when it contributes to avoid competition, being detrimental otherwise. Highest migration rates result in a more heterogeneous metapopulation distribution of the generalist consumer, indirectly supporting its specialist competitor. We discuss conceptual and methodological aspects of the model, demonstrating the importance of an integrative view. We also emphasize the relevance of vertical connections, suggesting how such a modelling framework could support conservation biology. Further studies should focus on methods to approximate external pressures with changes in model parameters, thus allowing to characterize possible impacts on ecological systems.

Keywords: social network; food web; landscape graph; hierarchy; stochastic simulation; individual-based modelling.

1. Introduction

The hierarchical organization of biological systems is well known, both below and above the level of the individual organism. Still, because of the multi-disciplinary and integrative nature of the problem, not too many studies focus explicitly on linking different organizational levels [1–3].

From a network perspective, it is clear that the structure of the social network formed by interactions among the individuals can be related to group dynamics and ecology of the population [4–6]. For example, Lusseau [4] suggests that a heterogeneous interaction network structure increases the relative importance of a few individuals in the group. Social structure can be related to communication among
the individuals over large distances: in case of elephants, the spatial dynamics of the population is also related to the fine structure of the social network, at several levels [5]. Barton et al. [7] have shown that social group coherence is related to predation pressure: the fragmentation of the social network of baboon groups can increase if the density of predators is lower.

Also, interspecific interactions have effects on spatial community dynamics (see [8] for butterflies, [9] for pitcher plants and [10] for beetles). In butterfly associated metacommunities, van Nouhuys and Hanski [8] present the competition/ dispersal trade-off and several other multi-species interactions linking the community and the landscape level. For pitcher plant metacommunities, it was shown how different migration abilities cause species sorting and, thus, generate differences between local pitcher plant communities [9]. A systematic study on beetle metacommunities has shown that low dispersal rates are associated with more stable local communities [10].

Changes at landscape level can have fundamental effects on local communities and populations [11–15]. The famous example of coyotes and shrub-living birds [13] demonstrated how habitat fragmentation results in small isolated patches where top-predators can be locally absent, triggering mesopredator release and finally the local extinction of lower-level species (birds, in this case). Isolation is an extreme case but it can be considered as changing the migration rate to zero.

These vertical, intra-level effects tie together different organizational levels and integrate the myriads of horizontal interactions into a single multi-layer ecosystem.

The interplay of horizontal and vertical effects is an essential property of living systems and modelling this can shed more light on better understanding the diversity and vulnerability of natural ecosystems (and food web assembly [16]). For example, the trade-off between competition ability and mobility [17], the local extinction–recolonization dynamics [18] or extinction following inbreeding [19] are well-known evolutionary phenomena. Since there can be massive individual-level variability in the frequency of inter-specific interactions (e.g., trophic habits differ between individuals, see Bolnick et al. [20]), taking an individual-based modelling approach is quite reasonable here. It is increasingly recognized that variability itself has a great conservation value [21], since it is of extreme importance for adaptability and evolvability. Especially in the case of small populations, focusing on mean population values there is the risk to lose essential information on variability.

In this paper, (a) we present an individual-based, stochastic, dynamical modelling framework, where social networks of conspecific individuals represent the building blocks of food webs that are spatially linked in a landscape graph (resulting in a metacommunity; see Box 1). We model network dynamics at all of these three levels. Then, (b) we simulate the behaviour of this hierarchical network model and perform sensitivity analysis on it. Based on this, (c) we study the dynamics of the metapopulations of each species in the food web and present their sensitivity to changing population, community and metacommunity parameters of a particular species. Since the model is very complicated and characterized by a large number of parameters, we deliberately narrow our interest to the local perturbation of one particular parameter set. Finally, (d) we discuss the advantages and caveats of this framework and argue for its importance in future conservation science.

2. Methods

2.1 The model

We constructed a hierarchical model where population, community and metacommunity dynamics are simulated (Fig. 1). Population demography is regulated by birth and death rates. Conspecific individuals can be linked to each other to form a social network. The social networks of various species are
Box 1. Glossary

**Primary producers**: species that do not feed on other species (e.g., most of the plants).

**Consumers**: species feeding on other species (e.g., animals and carnivorous plants).

**Top-predators**: species that no other species feeds on (i.e., species at the top of the trophic chain).

**Social network**: a network of individuals as nodes, where edges are social relationships (e.g., interactions oriented towards food search and processing, or responsible for mechanisms of group vigilance/predator avoidance).

**Food web**: a network where nodes stand for species (or trophic components), and edges represent predator–prey (trophic) interactions.

**Landscape graph**: a network of habitat patches as nodes, with edges representing the ecological corridors that link the patches.

**Local population**: conspecific individuals coexisting in a habitat patch (i.e., a discrete area of habitat).

**Local community**: coexisting local populations in a habitat patch. These local populations belong to different species that interact in a single habitat patch.

**Metapopulation**: a set of local populations belonging to a species and linked by the regular dispersal of individuals between them.

**Metacommunity**: a set of local communities linked by the regular dispersal of individuals of several species between them.

**Local extinction**: the disappearance of a local population from a habitat patch.

**Global extinction**: the disappearance of a species from all habitat patches it inhabited previously.

**Network topology**: the neighbourhood relationships describing what is connected to what, independently of all other kinds of information. It illustrates the structure of the network, showing how the nodes are connected with each other.

**Complete graph**: a network where each node is linked to all other nodes.

dynamical: ties can be formed and broken. Besides creating and removing social ties, individuals are involved in food web interactions (i.e., trophic relationships with individuals belonging to other species). We consider food webs composed of five species: the top-predator E consumes specialist (C) and generalist (D) prey that feed on a single (A) or two (A and B) primary producers, respectively. This food web topology has been well-studied earlier [22]. The five habitat patches in the fully connected (i.e., complete) landscape graph contain these food webs of fixed topology. Possible resources are defined, for each consumer, by the fixed topology of the food web. However, the number of individuals and the strength of interspecific interactions do differ and are dynamical. Migration rates that regulate the mobility of individuals among the five patches are determined for each species.

Demographic parameters contribute to change the population size in the five patches, thus affecting trophic relationships and spatial dynamics. Structural properties of the social network influence food web dynamics: more dense social networks provide a positive feedback at community-level by
Fig. 1. The hierarchical structure of the model. Every population is composed of a social network of individuals (shown for species D). In each patch, the local community consists of five species: A and B are primary producers, C and D are primary consumers and E is top-predator. Five patches constitute the fully connected landscape graph.

both increasing the efficiency of the predators in capturing prey, and enhancing the predator avoidance. Trophic relationships shape the population size leading to prey death and, in certain cases, predator reproduction. Migration rates mould population size in each patch and spatial distribution of species at landscape-level.

2.1.1 Structure

2.1.1.1 Population level: demographic properties and social network interactions. Species $i$ is characterized by the $\text{init}_i$ initial number of individuals. For each species, initial population size ($\text{pop}_{i,t} = \text{init}_i$, at time $t = 0$) is spatially homogeneous in all five patches and differs only between species. Population dynamics is governed by (spatially homogeneous) birth ($b_i$) and death ($d_i$) rates, but can also be affected by community-level interactions (i.e., trophic relationships in the food

<table>
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<th>Parameters changed for species D</th>
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<td><strong>Population level (demography)</strong></td>
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<td><strong>Social network</strong></td>
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<td>- Probability of social tie formation &amp; removal ($p_o &amp; q_o$)</td>
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<td><strong>Community level (food web)</strong></td>
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<td>- Ratio of D consumption rates ($e_{DE}/e_{AD}$)</td>
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<td>- Predation losses to predator E ($e_{DE}$)</td>
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<td><strong>Metacommunity level (landscape graph)</strong></td>
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<td>- Migration rate ($m_o$)</td>
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webs that lead to prey death/resource removal, and can also trigger predator/consumer reproduction) and landscape-level dynamics (i.e., migration determines the population size of species in the five patches).

If \( i \) is a primary producer (species A and B in Fig. 1), the reproduction rate at time \( t + 1 (rrPP_{i,t+1}) \) is obtained by multiplying a constant birth rate \( (b_i) \) with the population size at time \( t (popPP_{i,t}) \) (1). Reproduction rates of consumers (species C, D and E in Fig. 1) are always associated to feeding events (i.e., a consumer can either ‘eat’, or ‘eat and reproduce’). The reproduction rate of consumer \( i \) at time \( t + 1 (rrC_{i,t+1}) \) is computed as the product of a constant ‘eat and reproduce’ rate \( (er_{ji}) \) with the population size of the consumer \( i \) at time \( t (popC_{i,t}) \), the population size of the resource \( j \) at time \( t (popR_{j,t}) \) and the ratio of the social network densities of consumer \( i \) and prey \( j \) at time \( t(D_{i,t}/D_{j,t}) \) (2).

\[
rrPP_{i,t+1} = popPP_{i,t} \cdot b_i, \tag{1}
\]

\[
rrC_{i,t+1} = popC_{i,t} \cdot popR_{j,t} \cdot er_{ji} \cdot \frac{D_{i,t}}{D_{j,t}}. \tag{2}
\]

The mortality of the individuals of species \( j \) is a function of either predation or internal mechanisms (e.g., aging). At time \( t + 1 \), the mortality of the individuals belonging to species \( j \) and eaten by the predator \( i (mort_{j,t+1}) \) is related to the population size of consumer \( i (popC_{i,t}) \) and resource \( j (popR_{j,t}) \) at time \( t \), regulated by a constant predation rate (either ‘eat’ = \( e_{ji} \) or ‘eat and reproduce’ = \( er_{ji} \)) and modulated by the ratio of the social network densities involving the individuals that belong to consumer \( i (D_{i,t}) \) and resource \( j (D_{j,t}) \) (3a), (3b). Otherwise, internal mortality of primary producers \( i \) at time \( t + 1 (mortPP_{i,t+1}) \) is computed as the product of a constant death rate \( (d_i = b_i/1000) \) by the square of the population size of species \( i \) at time \( t (popPP_{i,t}) \) (4). When \( i \) is a consumer, its internal mortality (i.e., not related to any feeding interaction) at time \( t + 1 (mortC_{i,t+1}) \) is linearly proportional to population size at time \( t (popC_{i,t}; \text{death rate} = dC_i) \) (5). Death by predation and other causes do not concurrently apply and represent two separate events.

\[
mort_{j,t+1} = popC_{i,t} \cdot popR_{j,t} \cdot e_{ji} \cdot \frac{D_{i,t}}{D_{j,t}}, \tag{3a}
\]

\[
mort_{j,t+1} = popC_{i,t} \cdot popR_{j,t} \cdot er_{ji} \cdot \frac{D_{i,t}}{D_{j,t}}, \tag{3b}
\]

\[
mortPP_{i,t+1} = popPP_{i,t}^2 \cdot d_i, \tag{4}
\]

\[
mortC_{i,t+1} = popC_{i,t} \cdot dC_i. \tag{5}
\]

Conspecific individuals of species \( i \) can establish social connections with each other. Social connections of population \( i \) are dynamically added with a social tie formation rate \( p_i \) (that stands for the probability of adding a non-existing link to the social network) and decrease by rate \( q_i \) (probability of removing an existing link from the social network). For the population of species \( i \), the effective rates of formation \( (linkF_{i,t+1}) \) and removal \( (linkR_{i,t+1}) \) of social connections at time \( t + 1 \) depend on the number of missing \( (\text{non \_links}_{i,t}) \) (6) and existing \( (\text{links}_{i,t}) \) (7) social links at time \( t \), respectively.

\[
linkF_{i,t+1} = p_i \cdot \text{non \_links}_{i,t}, \tag{6}
\]

\[
linkR_{i,t+1} = q_i \cdot \text{links}_{i,t}. \tag{7}
\]
At time $t$, the social network density of the individuals of species $i$ ($D_{i,t}$) is computed as the ratio between existing links ($2 \cdot \text{links}_{i,j}$; we doubled the number of links because, in presence of an undirected graph, each social interaction corresponds to two non-zero entries in the adjacency matrix) and all possible social connections ($\text{pop}_{i,t} \cdot (\text{pop}_{i,t} - 1)$; self-loops are not allowed) \(^{(8)}\). We also added a constant value to the denominator (0.001) to avoid a division by zero (see Supplementary Materials S1).

$$D_{i,t} = \frac{2 \cdot \text{links}_{i,j}}{[\text{pop}_{i,t} \cdot (\text{pop}_{i,t} - 1) + 0.001]}.$$ \(^{(8)}\)

In stochastic simulations, some variance can be observed when comparing the social network densities (related to the same population) during different runs, even if we used the same constant values for social link formation and removal ($p_i = q_i$). The social network needs not to be a connected graph (isolated individuals can exist); its density drives population dynamics and affects trophic interactions (see equations \((2-3b)\)).

### 2.1.1.2 Community level: trophic interactions in the food web.

In the food web, we considered the direction of trophic links, and dynamical effects can spread in both bottom-up and top-down directions. Food web connectance ($C$) in a community composed of $S$ species is computed as the ratio between existing trophic links ($l$) and all of the possible trophic interactions in the food web ($S^2$; i.e., also self-loops are allowed) \(^{(9)}\). Food web connectance is preserved in all landscape patches and equals 0.2 (as we considered directed trophic links that leave the prey and enter the predators); it represents the architecture of all the food web links that dynamically govern predator–prey interactions.

$$C = \frac{l}{S^2} = \frac{5}{5^2} = 0.2.$$ \(^{(9)}\)

Food web links are characterized by well-defined base rates of interaction. We denoted these values by the names of species involved in the trophic relationship (e.g., $e_{ij}$ stands for the rate of the feeding interaction involving the consumer $j$ and the resource $i$, in absence of reproduction).

At time $t$, the population sizes of consumer $j$ ($\text{pop}_{Cj,t}$) and resource $i$ ($\text{pop}_{Ri,t}$) influence the probability of a trophic interaction involving the two species. This probability can simply regulate trophic activities that satisfy the energetic needs of the consumer ($\text{eat}_{j,t+1}$) \(^{(10a)}\) or also cause its reproduction ($\text{eat\_repr}_{j,t+1}$) \(^{(10b)}\). These events are positively and linearly regulated by the social network density of $j$ ($D_{j,t}$), while a linear negative relationship exists with the social network density of $i$ ($D_{i,t}$). Constant base rates regulate in a positive and linear way the ‘eat’ ($e_{ij}$) and ‘eat and reproduce’ ($er_{ij}$) dynamics.

$$\text{eat}_{j,t+1} = \text{pop}_{Cj,t} \cdot \text{pop}_{Ri,t} \cdot e_{ij} \cdot \frac{D_{j,t}}{D_{i,t}}.$$ \(^{(10a)}\)

$$\text{eat\_repr}_{j,t+1} = \text{pop}_{Cj,t} \cdot \text{pop}_{Ri,t} \cdot er_{ij} \cdot \frac{D_{j,t}}{D_{i,t}}.$$ \(^{(10b)}\)

Both of these equations also serve to quantify the probability of prey $i$ death following a feeding event; see analogies with equations \((3a)\) and \((3b)\). Equation \((10b)\) also refers to reproduction rates of predator $j$; see equation \((2)\).
2.1.1.3 **Metacommunity level: migration rates in a complete landscape graph.** Each species $i$ forms a metapopulation, where the migration rate is $m_i$ (for simplicity, migration rates are spatially homogeneous). The words ‘migration’ and ‘dispersal’ can be used interchangeably, but in the text we always refer to ‘migration’. The landscape graph is a complete graph for each species, thus, we modelled metacommunities from a mass effect perspective (i.e., we focused on the immigration and emigration dynamics of local populations, and not on landscape graph topology) [23–25]. At time $t+1$, effective migration rate of species $i$ ($mr_{i,t+1}$) is proportional to a constant migration rate parameter ($m_i$) and changes according to the population size at time $t$ ($pop_{i,t}$) (11). All events that dynamically modify the population size of the species in the five patches contribute to affect the intensity of migration rates (e.g., reproduction and mortality rates at population level, and strength of feeding relationships in the food web community).

$$mr_{i,t+1} = pop_{i,t} \cdot m_i.$$  

(11)

2.1.2 **Dynamics** Simulations were carried out with BlenX, a programming language that is based on the process calculus Beta-binders [26]. BlenX language is stochastic and the programme is executed with the Gillespie SSA algorithm [27]. In BlenX, individuals are represented by boxes. These boxes are composed of a set of interfaces/binders (i.e., binding sites) that allow interactions between individuals (e.g., the interfaces contribute to establish social interactions with conspecific individuals, or define prey preference/affinity). Boxes also have an internal programme that drives the behaviour of each individual (e.g., it includes instructions for birth/mortality rates, or defines the probability of migration).

The BlenX code is composed of three files (see Supplementary Materials S1): the first defines the model (.PROG); the second declares the functions (.FUNC); the third summarizes the types (.TYPES). The .PROG file is made up of the header info (they indicate the number of steps that the simulator will schedule and execute, and specify a delta parameter to record events only at a certain frequency), a list of declarations (which summarizes: boxes—e.g., species individuals; interaction capabilities—e.g., they define predator–prey interactions or determine the formation of new social connections with conspecific individuals; internal control mechanisms—e.g., reproduction following the feeding activity), events (statements that have to be executed with a specified rate and/or when some conditions are satisfied—e.g., ‘spontaneous’ reproduction of the primary producers), the keyword run and a list of starting individuals (where the initial population size of each species in the five patches is set). The .FUNC file holds the constant definitions (e.g., feeding preferences of a predator for its prey) and quantifies rate functions (i.e., interaction rates or probability of events that are computed with a function, instead of being simply defined by a constant value—e.g., the migration rate of a species is given by the product of the population density in a patch with the constant migration rate parameter). The .TYPES file stores all the binder identifiers that can be used, and the affinities between binders associated with a particular identifier (e.g., it summarizes that species D can feed on A and B, by also declaring feeding preferences—i.e., affinities—that characterize each trophic interaction). Affinities can be defined by simple constant values or more complex functions. They govern the dynamical evolution of the model by affecting interactions between individuals (that are characterized by specific binder identifiers) and do not require to know the exact address of the interacting individuals.

Three main advantages are related to the use of BlenX: (a) it permits avoiding any global policy on the usage of names in order to make individuals interact; (b) it relaxes the style of interaction of exact name pairing; (c) it allows composability (i.e., models can be built in a modular way), with interaction information listed in a separate file (.TYPES) that can be edited or modified without altering the programme (.PROG file).
In BlenX, we implemented an individual-based description [28–30] of the hierarchical system. This allows performing stochastic simulations based on simple kinetic laws between the boxes representing the organisms [31]. In the model, primary producers have a net positive reproduction rate (given by the positive difference between birth and death rates), and they are assumed to reproduce autonomously (1). Animals have a net negative reproduction rate, but they can reproduce with some rate after eating (i.e., they have a fixed death rate that is independent from trophic interactions, while reproduction is constrained by the occurrence of feeding activity). In absence of trophic interactions, the population size of primary producers would continuously increase (i.e., they are not limited by resource availability), while consumers would go to extinction. Feeding interactions contribute to keep the equilibrium where primary producers do not exponentially grow, and consumers do not go extinct. Social tie formation and interspecific (trophic) interactions are described as affinities between boxes, while migration is represented by changes in internal states of the boxes. We adopted simple kinetic rules to describe trophic interactions. A trophic interaction is always proportional to the population size of prey and predators. It leads to the death of the prey and, possibly, to the reproduction of the predator (see equations (10a) and (10b)). We did not consider other functional responses (e.g., Holling types II and III) or asymmetric feeding interactions (e.g., we did not model small herbivores that damage large and modular plants by reducing their mass, without leading to death).

2.2 The simulations

For simulating the dynamics of the hierarchical system, we needed a parameter set that allowed all populations in the five patches to persist. First, we gathered empirical values from literature for the parameters that are essential to describe the dynamics. This dataset served to construct a preliminary ‘base model’. Then, we evolved the parameters of the ‘base model’ set through particle swarm optimization (PSO) [32]. We assembled a ‘reference model’ with all populations at equilibrium (i.e., no species go to extinction or continuously grow during simulation runs). Finally, we used the ‘reference model’ to carry out sensitivity analysis (with a focus on the generalist species D). We aimed at understanding the impact of population-, community- and metacommunity-level parameters on metapopulation size and spatial heterogeneity.

2.2.1 Parameter search All parameters we used vary in nature among different species and in different ecosystems. There is no straightforward way to build a ‘universal’ model based on typical parameter values for social link formation, predation and migration. Apart of variability and lack of data, the available datasets often describe different systems; there is no hope to find all necessary information about a single, particular three-level hierarchical system. Data at different levels of the model typically describe different kinds of systems: most social network data represent vertebrates or insects [4], most food webs describe wet ecosystems [33] and most landscape ecological studies focus on some particular organisms like carabids [34].

Data from literature include details concerning population size in landscape patches, social network interactions (i.e., density of the network and probability of social tie formation), food web structure (i.e., connectance) and dynamics (strength of trophic interactions), and landscape graph architecture (density of the networks) and dynamics (migration rates). These values served to assemble the ‘base model’ which was completed with arbitrary birth and death rates (see Table 1 for numerical values and references). In certain cases, the values in the ‘base model’ correspond to what is in the literature (i.e., food web connectance equals 0.2—see equation (9)—and fits well with a realistic range). Migration
Table 1 The values of the parameters found in literature and used in the ‘reference model’. Population level (demography): for each species we listed the initial population size (init) in the five patches; birth (b) and death (d) rates were arbitrary chosen and consumers (i.e., species C, D and E) cannot reproduce in absence of feeding activity; death rates of consumers correspond to their base birth rates (see Supplementary Materials S1). Population level (social networks): we set a constant rate of social tie formation and removal (p = q); density of the social networks (D_s) dynamically changes during simulations and this is why no values are indicated for the ‘reference model’. Community level (food web): feeding rates can either simply determine prey death (i.e., \( e_{AC} \), \( e_{AD} \), \( e_{BD} \), \( e_{CE} \), \( e_{DE} \)) or be also responsible for the consumer reproduction (i.e., \( e_{AC} \), \( e_{AD} \), \( e_{BD} \), \( e_{CE} \), \( e_{DE} \)); food web connectance (C) does not affect system dynamics, but defines the architecture of the five food web interactions. Meta-community level (landscape graph): migration rates in the ‘reference model’ (m) are representative of the literature values; the density of the landscape graph (D_L) equals 1 (i.e., the landscape graph is a complete network). Food web connectance and network densities (for social network and landscape graph) are dimensionless. All the other parameters are expressed as probabilities, except the initial population size (which indicates the number of individuals).

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<th>Literature Value</th>
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rates found in the literature range from 0.01 to 0.5; we used values in this range (0.01–0.08) for species at higher trophic levels (i.e., species C, D and E) but values smaller by an order of magnitude (0.001) for the lower trophic level species. The reason is that most literature data describe lower migration rates for species at lower trophic levels [53,54].

Since we aimed to perform sensitivity analysis in a close to equilibrium state, we needed to refine our initial parameter set (without this, several components can go extinct or increase exponentially, making sensitivity analysis meaningless and impossible). We applied an evolutionary approach based on PSO [32] to evolve the parameter set of the ‘base model’. Once a proper fitness function is defined (i.e., a stable behaviour of the system), the PSO algorithm iteratively selects the most promising regions in the parameter space until convergence criteria are met. Every parameter guess is evaluated using the fitness function on the results of stochastic simulations. By using this evolved parameter set we defined a ‘reference model’ (see Table 1). Simulation outcomes of the ‘reference model’ are much more consistent than before and ready for meaningful sensitivity analysis. Such a hierarchical dynamical model can hardly be created by using much less parameters. However, because of the high number of parameters, the parameter space is huge and it is clearly impossible to systematically map it. One option is to sample it in a mathematically defined way (which is ‘biologically blind’). Another option is to map the neighbourhood of biological datasets (which is technically probably less elegant). The latter approach could be favoured by biologists, but because of the general lack of data, it is still simply impossible. We chose a hybrid approach: we tried to define biologically meaningful values and performed a standard screening of parameters. Although our main objective was relying on a single parameter set that allowed populations to persist, we also aimed at selecting this set in the most realistic way (this is why we started with real parameters from the literature, and then evolved the parameter set through PSO).

2.2.2 Sensitivity analysis. To carry out sensitivity analysis we focused on the dynamics of species D. We aimed at analysing the sensitivity of all species to changing six parameters that govern the dynamics of D at the three hierarchical levels. At population-level, we modified the initial number of individuals (i.e., initial population size: $\text{init}_D$), the death rate ($d_D$; see equation (5)) and the probability of social tie formation and removal ($p_D$ and $q_D$; see equations (6) and (7)). At community-level we analysed the consequences of generalist vs. specialist trophic activities (ratio of D consumption rates, with respect to species B and A: $e_{BD}/e_{AD}$; see equation (10a)), and impacts related to changes in predation losses to predator E ($e_{DE}$; see equation (10a)). To test the relevance of metacommunity-level dynamics we checked different migration rates ($m_D$; see equation (11)). We modified the parameters of the ‘reference
model’ to perform sensitivity analysis. We always tested 15 alternative values to explore the surrounding of the 6 ‘reference model’ parameters (i.e., the average of the scanned parameter values was close to the parameter value in the ‘reference model’, except for the social tie formation and the feeding preferences of D; often, we used the ‘reference model’ value as the barycentre of the scanned ones; see Supplementary Materials S2).

For each parameter value we ran 100 simulations (i.e., a set of 15 values required 1500 simulation runs, for testing the sensitivity to a specific parameter). We sampled the time-series after 60 steps. Based on the chosen parameter values, this simulation time corresponds to the time-scale of 2 months. To evaluate the results of the simulations, only the population size in the second-half of the time series was used (i.e., after a supposed transient phase). Average population size and coefficient of variation (CV; i.e., the ratio between standard deviation and the mean) were computed for each species in the five patches, using the data extracted from the 100 simulations (i.e., they were measured over the second-half of the time series; see Fig. 2(a)). This strategy is the best as it avoids too volatile results (e.g., by using only the last point of the time series, the results could be strongly affected by the initial conditions) and minimizes risks of transient dynamics (i.e., possible limit associated to the analysis of the entire time series).

Using the average and the CV over the second-half of the 100 time series, we ended with two sequences of 25 values (Fig. 2(b)). They describe the sensitivity analysis outcomes for a scanned value of a specific parameter. To summarize sensitivity analysis of each parameter we created two matrices (one for the average values and the other for the CVs) of 15 rows (one for each value scanned) and 25 columns (showing results for five species in five patches). Response variables were finally extracted from the matrices obtained for the six parameters through simulations (i.e., six matrices describing average values and six matrices summarizing CVs). In case of average values, response variables are classified as metapopulation size and spatial heterogeneity (Fig. 2(c)). Metapopulation size refers to the row sum of the five average population sizes in the five patches, while the spatial heterogeneity quantifies the row CV of the five average population sizes in the five patches. We also measured sum and spatial heterogeneity (i.e., CV) of the intra-patch variability.

3. Results

We measured fluctuations in metapopulation size and spatial heterogeneity of five species distributed among five habitat patches. To quantify the effects of population, community and metacommunity-related mechanisms we performed sensitivity analysis on parameters describing the behaviour of species D. For each species in the five patches, we computed average and CV of the population size, over the second-half of the simulated time series (see Supplementary Materials S3). We found that food web processes have the weakest effects on metapopulation size and spatial distribution of species, while parameters regulating population and metacommunity dynamics are of at least comparable magnitude.

In Fig. 3, we illustrate how the metapopulation size of D (scenario ‘MS’, Fig. 2(c)) is modulated by changes in: frequency of social tie formation and removal (population-level); degree of feeding specialization (community-level); intensity of inter-patch migration (metacommunity-level). Highest rates of social tie formation generate less cohesive social networks, resulting in smallest metapopulation size. Species D feeds on species A and B; it is the only consumer of B, while it competes with species C for A (Fig. 1). We explored a gradient of feeding solutions ranging between the specialization on either A or B. All the simulated feeding strategies have a weak impact on the average metapopulation size of species D (i.e., they are responsible for changes in the range of ∼3%), showing a weaker effect than the probability of social tie formation (for which a drop from more than 26 individuals to
Fig. 2. Sensitivity analysis. We evaluated the effects of six parameters that describe species D dynamics at three hierarchical levels (population, community and metacommunity). (a) For each parameter we checked 15 values by running 100 simulations per value (i.e., altogether we performed 1500 simulations for each parameter). (b) Consequences on the population size of the five species in the five patches were measured as average or CV over the second-half of the 100 time series simulated for each value. For each parameter, we obtained two matrices composed of 25 columns (five species in five patches) and 15 rows (one for each checked value). (c) Metapopulation size refers to the sum of the five average population sizes in the five patches and spatial heterogeneity quantifies the CV of the five average population sizes in the five patches. We also estimated the sum of the intra-patch variability (row-sum of the five CVs in the five patches) and the spatial heterogeneity of the intra-patch variability (CV of the five CVs in the five patches).

<16 is observed when moving from $P_D = 0.1$ to $P_D = 0.3$). Strict specialization on A is detrimental, while largest metapopulation sizes correspond to diets more specialized on B. Generalist trophic habits (i.e., at intermediate values of the x-axis) often lead to a large metapopulation size, although a minimum is observed when the feeding preference of D for A equals 70% ($e_{BD}/e_{AD} = 0.3/0.7 = 0.429$). An optimum range of migration rates allows better persistence of species D, while too intense inter-patch movements impair the metapopulation size. The peak in the metapopulation size is in the range of biologically realistic values ($0.01 \leq m_D \leq 0.5$). Effects of changes in other parameters describing demography and community-level dynamics of species D are shown in Supplementary Materials S4. Initial local populations determine small impacts on the metapopulation size of D. A sharp decrease in the metapopulation size of D corresponds to highest mortality rates; this intuitive pattern contributed to validate the soundness of the model structure. Low predation rates of the top-predator E are associated to largest metapopulation sizes of D.

Besides characterizing the impacts on metapopulation size, we quantified the consequences on spatial heterogeneity (see Fig. 4 that refers to scenario ‘SH’ of Fig. 2(c)). In case of social tie formation and removal, spatial distribution displays a rather regular pattern that is independent of the social network density (i.e., on average, we observed differences accounting for 10% of the metapopulation size); exceptions correspond to $P_D = 0.3$ and $P_D = 1.0$. Highest spatial variability is found with trophic specialization, while a more predictable spatial distribution matches the generalist trophic behaviours. Migration rates below the threshold of $m_D = 0.5$ correspond to spatially homogeneous distributions; beyond this limit, the populations are unevenly distributed among the five habitat patches. Supplementary Materials S5 includes plots on spatial heterogeneity controlled by demographic and community-level parameters. Lowest heterogeneity is observed with highest death rates. A more heterogeneous metapopulation distribution (i.e., spatial specialization) is related to intermediate sizes of initial local populations and highest predation rates of E. In Supplementary Materials S6 and S7, we show total intra-patch variability and spatial heterogeneity of the intra-patch variability (see scenarios ‘IPV’ and ‘SHIPV’, Fig. 2(c)).

We also investigated the consequences on the metapopulation size of different food web species (see Fig. 5). More rapidly changing social relationships impair the feeding activity of D, with an advantage for the primary producer B; this triggers a (bottom-up) cascade effect (starting from D), ending with smallest metapopulation size for the top-predator E. Specialization on the primary producer A (which is a resource shared with C) and more generalist trophic behaviours have detrimental effects for species D. A direct positive mechanism regulates metapopulation size of B, while indirect effects prevail in the dynamics of top-predator E (which preferentially prey on C; prey C over-competes with D when this latter is more generalist; see Supplementary Materials S8). Highest migration rates determine a sharp decrease in the metapopulation size of D; a cascade effect depletes top-predator E metapopulation size, while species C over-competes and increases (i.e., apparent competition).
Fig. 3. Sensitivity of the metapopulation size of species D to parameters describing its dynamics at three hierarchical levels. For the ratio of consumption rates B/A, the x-axis is in log scale.

Fig. 4. Spatial heterogeneity of species D in response to changes in the dynamics at three hierarchical levels. The x-axis in the plot illustrating the ratio of consumption rates B/A is in log scale.

4. Discussion

The multi-level network simulation model illustrates the vertical (inter-level) relationships in the system. We constructed the model starting from real data that refer to different ecological systems, with the objective of studying how changes in a particular hierarchical level can affect the others (e.g., changed social network cohesion influencing metapopulation size and spatial distribution).

Social network theory has been recently suggested as a promising approach in behavioural ecology [55]. Group living can involve cooperative hunting [56] and information transfer about the location of high-value food sources [57]. Animal sociality can result in vigilance with information transfer (e.g., via alarm calls or predator inspection), thus enhancing predator avoidance and increasing foraging efficiency [58].

In our hierarchical model, populations characterized by more intense social tie dynamics are endangered because, on average, display lowest social network densities (i.e., less cohesive networks). Given the structure of the model (see equations (10a) and (10b)), sparse social networks reduce the efficiency of consumer feeding activity (thus simulating possible consequences of less cohesive social structures on food search and processing) and impair predator avoidance (by mimicking how less cohesive social networks can weaken mechanisms of group vigilance, group defence and confusion effect [59]). A decrease in the metapopulation size of D emerges in presence of more intense social dynamics (Fig. 3); in these conditions, a concurrent level of variability is preserved in spatial distribution (Fig. 4). More intense social relationships result in sparse social networks, without triggering clear changes in spatial
distribution. Also Pacala et al. [57] observed that high interaction rates can cause social groups to pursue unprofitable tasks. This finding is in agreement with our modelling outcome, although Pacala et al. mainly focused on the effects of social group size on social interactions and information exchange. They pointed out how the adaptability of larger groups to changing environment is likely to be more efficient as per capita rates of social interaction can increase with group size. However, they also showed that more intense social relationships can be detrimental for large groups (with population size larger than 100 individuals) as individuals become more involved in conspecific interactions at the expense of adapting to environmental conditions. The effects of such an unbalanced activity are more pronounced for large groups than for a small one (i.e., with population size smaller than 100). We found many similarities with our results where the initial population size of species D (in each patch) is well above 100 individuals (see Table 1), and the increase of tie formation and removal rates leads to a sharp decline of the metapopulation size (Fig. 3). Moreover, our simulations stabilized the population size of species D
below an average value of 10 individuals per patch. This happened in presence of very intense social relationships and is consistent with the findings of Pacala and colleagues. Given the same level of social activity, Pacala et al. described groups with 10 individuals as more stable than larger ones; their findings could justify the fact that our model reached a new equilibrium with smaller population size when individuals pertaining to species D were involved in more frequent social relationships.

To better understand whether less cohesive social networks of species D have more effect on the impairment of foraging efficiency or predator avoidance, we studied the metapopulation size of other species in the system (Fig. 5). The primary producer B benefits from the decreased feeding activity of its unique consumer D. D feeds with less efficiency on B and decreases its metapopulation size. This outcome is in agreement with the idea that individuals involved in too intense social relationships tend to undermine their adaptation to environmental conditions [57], thus failing to efficiently feed on resources. This generates a bottom-up effect that determines the concurrent drop in the metapopulation size of the top-predator E. The top-predator cannot offset this trend by simply feeding on D with more efficiency (i.e., this could be the consequence of the fact that it preserves its social network topology, thus being favoured by less cohesive social structures of D). Top-predator survival is therefore limited by the availability of the resources, rather than receiving an advantage by highest prey vulnerability. We observed a bottom-up regulation that, on the top-predator E, has analogous consequences to what is observed for pelagic fish in marine ecosystems [60]. The structure of our model includes the chance that such a kind of mechanism also originates from species social behaviour (and can be of comparable magnitude to other demographic-, community- and metacommunity-level effects; e.g., sensitivity to death rates and migration rates; see Fig. 3 and Supplementary Materials S4), rather than being solely regulated by food availability.

Trophic specialization of D generates two contrasting results when considering the effects on metapopulation size (Fig. 3). However, both of the cases are characterized by higher levels of spatial heterogeneity if compared with scenarios based on more generalist behaviours (Fig. 4). In the toy model as in real ecosystems, specialists tend to specialize on a specific habitat patch, while generalists use a greater diversity of habitat patches [61,62].

Several studies have been dedicated to a better understanding of the ecological traits that exacerbate the vulnerability of species to extinction. Within this framework, specialization and small population size are both believed to enhance the risk of extinction [63]. Our results confirm that specialization is the most dangerous strategy for species persistence, but only when D exclusively feeds on A (i.e., when it competes with C; see Fig. 3). This finding is in agreement with the literature suggesting that specialization is associated with highest risks of extinction [63,64]. However, specialization on B shows opposite and partially contra-intuitive effects: it contributes to raise the metapopulation size of both D and B, also sustaining the growth of the top-predator E (Fig. 5). The model illustrates how being specialized can be an efficient strategy under certain conditions (i.e., D avoids to compete with C). The positive feedback received by E is a consequence of the increased metapopulation size of D. A possible justification for the concurrent rise of B can be related to the structure of the social relationships of D. Larger metapopulations of D are not accompanied by a proportional increase in the number of social connections. Lower social network density found for the scenario of extreme specialization on B partially reduces the feeding efficiency of D. This complex pattern involves the spread of social network effects beyond the population-level dynamics and further demonstrates the relevance of the hierarchical approach. Although dietary specialization is mainly associated to highest risk of extinction, the dynamics simulated by our model is not unrealistic. For example, the persistence of specialized groups, at the expense of species implementing more generalist strategies, is described for ants in a fragmented landscape [65].
The specificity of the evolved parameter set (i.e., the fact that the model reacts with extreme sensitivity to small changes in certain parameter values; see in Table 1 the initial predation rates among the five species in the ‘reference model’) can suggest we are close to a local minimum. Therefore, the predation rates adopted in our model can show the extremes of the system, failing to be fully representative of its ‘average’ behaviour. This hypothesis is further corroborated by the fact that the sensitivity analysis carried out for the community-level parameters (ratio of D consumption rates and predation losses to predator E; see Figs 3 and 4, and Supplementary Materials S4 and S5) does provide less robust patterns than in the cases of population- and metacommunity-level parameters. This can be due to the fact that small changes in the predation rates push the system away from the equilibrium found with PSO. However, small changes (in absolute terms) observed with sensitivity analysis of community-level parameters could also stand for a highly representative configuration, despite the specificity of the evolved parameter set (i.e., they activate much less penetrant consequences on metapopulation size and spatial heterogeneity than population- and metacommunity-level parameters).

Understanding the evolution of migration rates and the wide diversity exhibited by animals and plants are major subjects of study in theoretical ecology. Concrete applications can involve the investigation of the mechanisms that lead to changes in the migration rates [66] and a better quantification of the extinction risks [67]. Many publications claimed for an optimum migration rate that emerges as a trade-off between energy consumed for migration and advantages associated to it (e.g., benefits can involve rescuing a metapopulation from extinction in a deteriorating landscape, or minimizing the predation risks) [66,67]. Other researchers showed how discontinuous areas (i.e., habitat fragmentation) threaten species persistence; in this case, extinction rates fall sharply when migration is increased from zero, but stabilize at highest migration rates [68]. Nonetheless, high migration rates can be as detrimental as low migration rates, for the fate of the metapopulation [69].

In our model, five landscape patches were connected in a complete graph (i.e., there are no effects of topological fragmentation). We simply modulated the intensity of migration for species D, thus mimicking possible consequences of fragmentation through a gradient of migration rates. For each scenario, we simulated homogeneous migration rates in the whole landscape graph. We observed how largest metapopulation sizes correspond to low-intermediate migration rates (Fig. 3). Highest migration rates do not contribute to synchronize the populations that are dispersed in the five patches (i.e., there is highest spatial heterogeneity; see Fig. 4), and also decrease the metapopulation size. Our results corroborate previous findings: an increase in the migration rate is not automatically associated to more persistent metapopulations [69]. The asynchrony generated by our simulations does not correspond to a concurrent raise in the metapopulation size. A possible explanation for the weak positive impact of migration on metapopulation size could be due to population density dependence [70]. Ives et al. [70] adopted a stochastic framework for investigating the effects of migration on population density. They concluded that the effect of migration on the population size is enhanced by (a) weak density dependence, (b) high environmental variability regulating population growth rates and (c) lack of synchrony between the populations in the habitat patches. In our model, we considered constant birth and death rates. Reproduction and mortality rates of consumers change as a function of their population size. They are also affected by the social networks of resources and consumers, but we did not explicitly consider the role of environmental variability (see equation (2)). Asynchrony emerges with highest migration rates (Fig. 4) but, contrary to what showed by Ives et al. [70], it is not enough for raising the metapopulation size. Therefore, we argue that intra-population competition (i.e., density dependence) can be responsible for the decrease of the metapopulation size. Another possible explanation of the discrepancies between our study and the findings of Ives et al. can depend on the structure of the model. As observed with the sensitivity analysis of social tie formation rates, the feeding
activity of D is highly compromised by low social network densities (see the small metapopulation size in Fig. 3). More heterogeneous spatial distributions (as the ones obtained with high migration rates) lead, in some patches, to extremely incohesive social structures. These result in less efficient consumers and smaller population size if compared with scenarios with low-intermediate migration rates.

Highest migration rates caused a more heterogeneous metapopulation distribution of the generalist consumer, indirectly supporting its specialist competitor (Fig. 5). This is because of the apparent competition mechanism regulating the coexistence of the two consumer species (C and D) that are both preyed upon by the same top-predator (E) [71]. The simulation framework was essential to capture such a kind of behaviour. Based on feeding preferences (Table 1), we would conclude that species C represents the preferential prey of the top-predator, thus being the ideal candidate for establishing an apparent competition control. Changes in migration rates of species D generate a different scenario. The more heterogeneous spatial distribution found for species D in presence of highest migration rates is also associated to less cohesive social structures. Given the architecture of the model (see equations (10a) and (10b)), species D becomes a more appealing food for the top-predator E. A decrease in the population size of D is therefore associated to a concurrent negative effect on the top-predator population size, relaxing the feeding pressure on the other consumer (i.e., species C).

5. Conclusions

We showed that, within the context of our modelling framework (model structure, parameter set and sensitivity analysis), changes at the bottom level (social dynamics) can impact the top level (metapopulation structure). Changes in food web dynamics caused the weakest effects, and this contra-intuitive finding illustrates the possibly similarly important role of population and landscape-level mechanisms, as well as the need for considering vertical mechanisms.

We found that rapidly changing social relationships generated less cohesive social networks and determined less effective consumption patterns. Other authors suggested that too intense social relationships can be detrimental of the population status, leading to lowest probability of success [57]. We also observed that less cohesive social groups were more affected in their feeding activity, rather than being more vulnerable to the predator attacks.

In our toy model, feeding specialization is an advantage when allows escaping competition, while it becomes detrimental in case competition is sharpened. Although some authors showed the possible advantages associated to a specialized feeding strategy [65], risks of extinctions are usually thought to be dampened by generalist trophic behaviours [63,64]. We noticed how highest spatial heterogeneity is associated to more specialized diets. Dietary specialization can provide a competitive advantage but this tends to be localized in specific habitat patches (i.e., it results in spatial specialization) [61,62], while generalist species are more homogeneously persistent.

An increase in the migration rates is not monotonically associated to a raise of the metapopulation size. By simulating the consequences of a range of migration rates we found an optimum (i.e., a peak in the metapopulation size) in correspondence of realistic values. We observed that highest migration rates can be as harmful as the lowest ones [69]. Other researchers showed how asynchrony enhances metapopulation size [70], but our simulations identified an opposite pattern (i.e., highest migration rates are associated to population asynchrony but lead to a decrease of the metapopulation size). Different criteria in model construction (e.g., the lack of environmental variability) can explain this discrepancy. Changes in migration rates also contributed to emphasize the presence of an apparent competition
mechanism. This provided an example of how indirect vertical effects can modulate community composition (i.e., different migration rates determine a change in the social structure of populations in habitat patches, thus affecting predator avoidance and feeding efficiency). Although these results depend on the architecture of the model, we argue that it is not unrealistic the presence of a link connecting the migration-dependent frequency of social relationships to population stability [55].

The presented model is, on one hand, over-simplified (e.g., sociality is represented only as the density of the social network) and, on the other hand, extremely complicated (many parameters). It was constructed using different data sources and did not aim at providing suggestions on how to manage a real system. Our main objective was illustrating possible interdependencies between the population, community and metacommunity levels, and quantifying their relative importance. Other details could be included and different equations adopted to better describe ecological processes involving the three layers. The presented version of the model is more like a framework that helps to understand how ecological effects can spread between hierarchical levels. Potential future extensions include exploring a larger region of the parameter space (with as much as possible real parameters). Also, the effects of landscape topology can be easily studied by structuring the landscape graph [34,72–74]. Importantly, we can add local instead of global determination for some parameters: for example, rates $p$ and $m$ can depend on food web position of species. On the other side, increased global determination can be explored by adding direct links between social networks and the landscape graph [75]. Modelling also vertical effects can contribute to better understanding the direct and indirect determination in ecosystems [76–78]. However, the large number of parameters and the need for real data (see a rare example for metacommunity data in [79]) are clear disadvantages.

Several studies aim to serve decision-making but most of them are of structural and static nature [80]. Our modelling framework will offer the possibility for integrating multiple sources of information for strategic conservation management. If a particular population is in extinction risk, the reason can be related to its internal structure (e.g., demography, sex-ratio, social structure), to its interspecific interactions (predators, parasites, competitors, scarcity of food) or to its spatial behaviour (source-sink structure, mobility, migration). Our integrative model, if realistically parametrized, can show the best way to manage multi-level systems: sensitivity analysis can indicate the critical parameters and suggest how to approach the problem, if able to quantify the strength of external pressures. Being able to connect changes in the values of some parameters to the magnitude of external pressures would give the chance of measuring these pressures in the simulations. This is just a hypothetical approach we did not implement in the manuscript. For example, if we consider a target species, pollution can decrease the initial population size, increase the death rate or reduce social dynamics, while habitat fragmentation can result in poor migration ability. The multi-level network simulation model can be an interesting and promising application for conservation practice on the long term.

6. Supplementary data

Supplementary data are available at Journal of Complex Networks online.

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