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A single changing hypernetwork to represent (social-)ecological dynamics

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ABSTRACT

To understand and manage (social-)ecological systems, we need an intuitive and rigorous way to represent them. Recent ecological studies propose to represent interaction networks into modular graphs, multiplexes and higher-order interactions. Along these lines, we argue here that non-dyadic (non-pairwise) interactions are common in ecology and environmental sciences, necessitating fresh concepts and tools for handling them. In addition, such interaction networks often change sharply, due to appearing and disappearing species and components. We illustrate in a simple example that any ecosystem can be represented by a single hypergraph, here called the ecosystem hypernetwork. Moreover, we highlight that any ecosystem hypernetwork exhibits a changing topology summarizing its long term dynamics (e.g., species extinction/invasion, pollutant or human arrival/migration). Qualitative and discrete-event models developed in computer science appear suitable for modeling hypergraph (topological) dynamics. Hypernetworks thus also provide a conceptual foundation for theoretical as well as more applied studies in ecology (at large), as they form the qualitative backbone of ever-changing ecosystems.

Keywords: Ecosystems, interaction networks, hypergraphs, Petri nets, discrete-event models.

Introduction

36 Ecosystems are under threat and we need to think carefully about their representations for many
37 reasons. A sound representation helps to conceptualize the study, to understand and ultimately, to
38 manage ecosystems. Ecological and epistemological works continually propose new representations of
39 these complex objects (Gignoux et al., 2011; Schwartz & Jax, 2011), such as class diagrams and
40 interaction networks (Strogatz, 2001; Loreau et al., 2003; Proulx et al., 2005), to name but two. Such
41 representations should firstly be useful and provide relevant insights. Secondly, even in case of well-
42 understood ecosystems, tracking their changes and managing them efficiently, necessitates dealing with
43 a reliable and intuitive representation. While redefining the ecosystem is outside the scope of this paper,
44 we at least acknowledge that all ecosystems are made up of biotic, abiotic and often anthropogenic
45 components. These components continuously interact through various (bio-ecological, social-economic,
46 physicochemical) processes (e.g., S. Frontier et al., 2008; Gignoux et al., 2011; Gaucherel, 2018). Defined
47 as such, the ecosystem may be, and often is, represented as a set of (material) variables and (abstract)
48 processes (Fontaine et al., 2011; Pilosof et al., 2017; Landi et al., 2018). While a set-based representation
49 does not assign an order to ecosystem content, matrix or graph representations more explicitly specify
50 their complex, directed (oriented) interconnections. Such representations often exhibit specific
51 structures, such as multiple interactions between variables (Sonia Kéfi et al., 2017; Gaucherel &
52 Pommereau, 2019) or nested (Bastolla et al., 2009) and modular sets (Dicks et al., 2002) of variables.

53

54 Species networks and social networks provide two textbook cases of network representations. It is
55 common to represent species communities in the form of a graph in which the main variables (species or
56 populations) are represented by nodes and their ecological interactions by edges. Species networks
57 generally consist in sub-systems of an ecosystem, including e.g., food webs, plant-pollinator networks,
58 host-parasite networks and competition networks. Some of these graphical models have also been
59 combined with a dynamic model to examine variations in species abundances and process flows (fluxes)
60 on the graph (Proulx et al., 2005; Delmas et al., 2018; Landi et al., 2018). The use of multilayer, multiplex
61 and multilevel networks has recently been proposed to merge distinct sub-systems in the same network
62 (S Kéfi et al., 2016; Pilosof et al., 2017). These multigraphs are representations combining several initially
63 separate graphs involving the same variables into a multilayered graph.

64

65 Latterly, it has been proposed to study *hypergraphs* for their ability to grasp non-dyadic (i.e., non-
66 pairwise) interactions between species, also called *Higher-Order Interactions*, as many ecological
67 interactions appear to be mediated by a third (or more) species (Werner & Peacor, 2003; Golubski et al.,
68 2016; Delmas et al., 2018). Such multi-component interactions thus play an important role in system
69 dynamics. Hypergraphs have rarely been used in biology and ecology (but see Billick & Case, 1994; Klamt
70 et al., 2009 ; Valverde et al., 2020). Several definitions have been proposed for the higher-order
71 interactions they capture: a dyadic interaction modulated by (i.e., in the context of) a third species, a
72 non-additive effect of two species on the per-capita growth of another, or the failure of a null dyadic
73 model (Sanchez, 2019). However, the hypergraphs and higher-order interactions found in the literature
74 are mainly confined to interactions made up of three components and are static. Here, we venture to
75 generalize that i) higher-order interactions not only concern species interactions, ii) are not at all
76 restricted to three-way interactions and, ultimately, iii) often change sharply in the long term. In parallel,
77 social networks are also much used and studied.

78

79 In the same vein as species networks, anthropogenic nets can be plotted in graph form, with which
80 humans or human groups shown as nodes and each human-related process (e.g., communication,
trading, financial exchange) as an edge connecting the concerned nodes (e.g., Buldyrev et al., 2010;

81 Brummitt et al., 2012). Depending on the question being addressed, such human-related graphs are
82 sometimes purposefully biased by more social, more economic or political processes. Rarely, these
83 interaction networks are merged into the same larger graph for study, such as in decision systems (Tixier
84 et al., 2013; Battiston et al., 2020; Felipe-Lucia et al., 2021). As humans in a society, we understand that
85 social networks are highly dynamic, frequently losing or gaining new components (individuals or groups)
86 and interactions, such as in ecosystem services (Scholes et al., 2013; Mao et al., 2021). In principle, there
87 is nothing to prevent the merging of interaction networks involving human groups with networks
88 involving species once they interact (Felipe-Lucia et al., 2021), and so on with any other (e.g.,
89 physicochemical) variable in the same social-ecological system.

90

91 In this paper, we will build on the representations above to put forward three interlinked
92 propositions: i) any ecosystem may be efficiently represented by a single graph, here called the
93 *ecosystem network*, whatever the interactions it involves; ii) this single graph would gain from being a
94 hypergraph (called *hypernetwork*), made up of non-dyadic interactions; and iii) the single hypernetwork
95 changes in the long term, hence the need to formally document these changes to improve our
96 understanding of ecosystem dynamics. In other words, we aim to show that the whole (social-)ecological
97 system (i.e., with all the processes and components it involves) can be represented by a single
98 comprehensive graph which may be more accurately defined as a changing hypergraph. In addition,
99 many ecological interactions are non-dyadic, i.e., they involve more than two variables and, reciprocally,
100 most variables are simultaneously involved in many interactions (Billick & Case, 1994; Valverde et al.,
101 2020). In this paper, we will not present new models and new results, rather than exemplify the
102 proposed concepts with our past basic (Gaucherel & Pommereau, 2019; Pommereau et al., 2022a) and
103 applied studies (Mao et al., 2021; Cosme et al., 2022). As a simple illustration, we will model a termite
104 population that is eating, producing mushrooms and reproducing through various processes (Turner,
105 2009). We will show the numerous advantages of representing the ecosystem as a changing
106 hypernetwork, and will discuss the conceptual, explanatory and practical insights it provides.

107

Methods and Results

108 A single graph for the ecosystem

109 To summarize any ecosystem on the basis of its interactions and interaction networks implies an
110 understanding, first and foremost, of what an interaction is. An interaction can be defined in several
111 ways, although most ecologists would accept that it is an abstraction of “real relationships” between
112 species or between any other ecosystem components (Delmas et al., 2018; Landi et al., 2018). For
113 example, a “predation interaction” takes the form of the catching and eating by (at least) one predator
114 individual of (at least) one prey individual (Nakazawa, 2020). Hence, what is usually called predation is an
115 abstract concept, a kind of immaterial process, with a duration in time and aggregating many events.
116 When ecologists study interaction networks to understand or predict their dynamics, they mostly explore
117 quantitative variations in variables (abundances) through various flows (matter and energy exchanges)
118 connecting them (Lobry & Sari, 2015; Nakazawa, 2020) (Fig. 1a).

119

120 Everything that has been said about species may pertain to any other component of a social-
121 ecological system, depending on the question being addressed. For example, the economic interaction
122 stating that “a producer sells their productions to a consumer” is composed of a number of occurrences
123 of isolated and observable sales between two social units (Strogatz, 2001; Gross & Sayama, 2009).
124 Similarly, the social interaction “a scientist communicates their results” is composed of a number of
125 utterances or sentences between the scientist and the audience. The fact that the scientist may

126 simultaneously be communicator, consumer and predator eating a salad for lunch, strongly militates in
127 favor of merging the respective social, economic and ecological networks in which they are involved
128 (Felipe-Lucia et al., 2021). The reverse is also true: many processes require several components to be
129 applied. To “communicate their results”, the scientist may use a computer, the salad they have eaten and
130 potentially studied, and the audience. Hence, as a first step, a single graph can be built in each social-
131 ecological system, depending on the question being addressed (Fig. 1b).

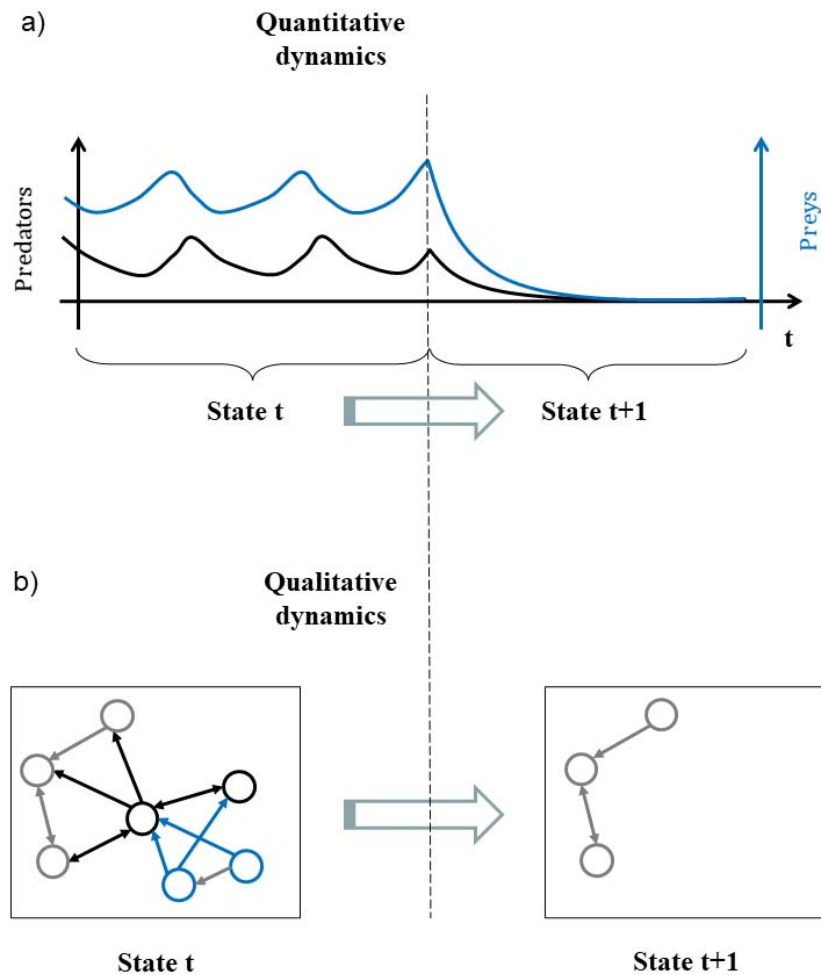


Figure 1

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133 **Figure 1** - Tentative representations of corresponding quantitative (a) and qualitative (b)
134 predator/prey dynamics. The total biomasses of predator (in black) and prey (blue) populations
135 fluctuate until they collapse (a). In the long term, the trophic network may be represented as a
136 qualitative graph, potentially involving other species (in grey), shifting sharply from one discrete
137 state to the next, lacking the corresponding prey and predator nodes.

138 In previous studies, we suggested calling this comprehensive graph the *ecosystem network* (EN)
139 (Gaucherel & Pommereau, 2019; Cosme et al., 2022), as it represents flows and is not simply an abstract
140 mathematical graph. This EN usually concerns a social-ecological system interaction network with no
141 limitations on the natures of its components and processes, insofar as the question being addressed
142 requires all these components. We illustrate here this proposed ecosystem representation with a
143 simplified theoretical termite colony (Table 1). Details of the models can be found in the literature
144 (Gaucherel & Pommereau, 2019; Gaucherel et al., 2020), and minimal information only will be given here
145 for understanding. The termite colony model consists in eight components (graph nodes, Fig. 2a)
146 connected through nine processes (edges), directed from the condition variables to the consequence
147 variables (Table 1). The same graph representing the system may be displayed with several algorithms for
148 highlighting distinct features (Fig. 2a-b), such as ecosystem boundaries or multiscale (nested) structures
149 (Montiglio et al., 2020).

150 All the graphs examined so far in various disciplines are indeed “sub-graphs” or modules of the same
151 single “super-graph” of the whole social-ecological system. Often, this is the same node of the EN,
152 representing a material component, which is potentially involved in highly distinct (trophic,
153 physicochemical and/or human-related) interaction networks (Fontaine et al., 2011; Gaucherel, 2019).
154 The reasons that we usually avoid merging all these modular graphs are: specific monodisciplinary
155 questions being addressed; data, knowledge or skills being unavailable; to avoid time-consuming analyses
156 often with limited capabilities; or for all these reasons combined. As seen recently in multilayer, multiplex
157 and multilevel analyses, individual graphs of the same system may be merged into a single larger graph
158 (Fontaine et al., 2011; Pilosof et al., 2017). This observation strongly suggests that each node is
159 connected to nodes of distinct natures, through interactions of various natures too (S Kéfi et al., 2016;
160 Gaucherel et al., 2020). In contrast to these studies, though, we do not make any hypothesis here about
161 the shape of the EN. It may be layered, modular, nested or have another specific structure: we do not
162 need to assume its shape, but instead allow the graph topology (i.e., the neighboring relationships) to
163 emerge from the purported, observed and known interactions (Mao et al., 2021; Cosme et al., 2022).

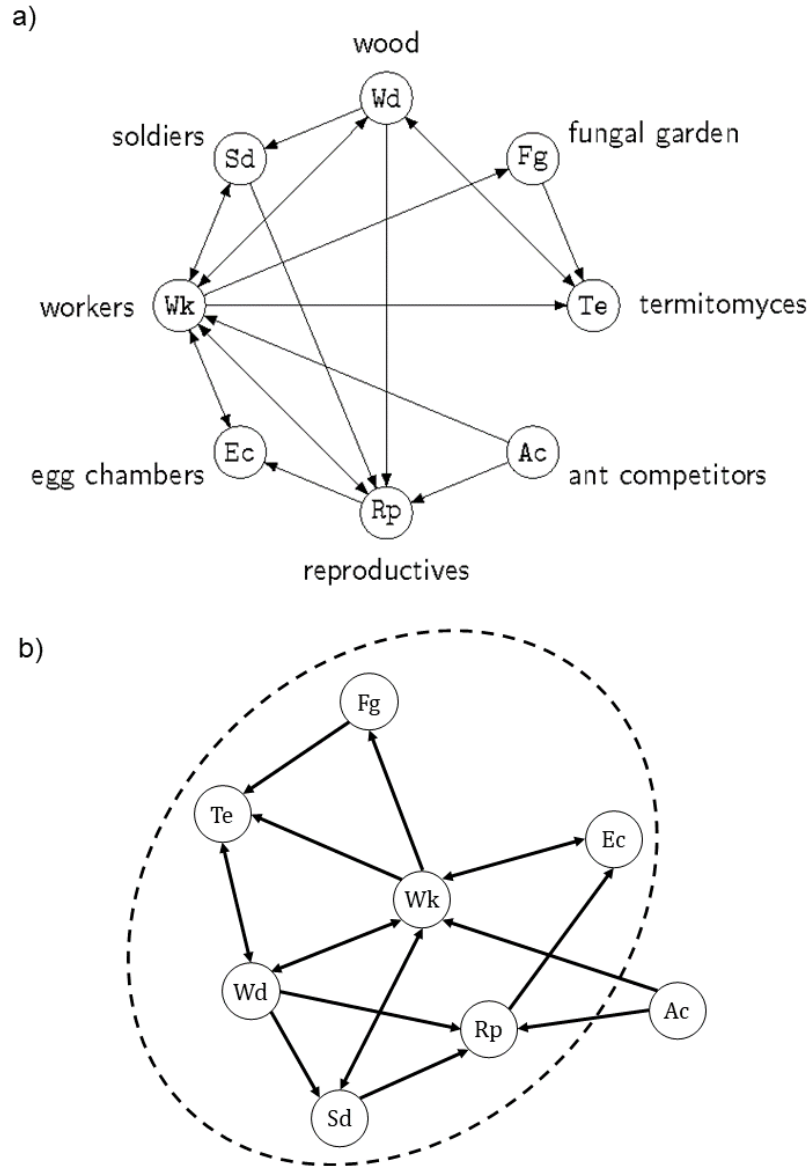


Figure 2

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Figure 2 - Two different representations of the same network of a termite colony ecosystem (a and b). In the first traditional representation (a), the eight variables (nodes, Table 1) and ten processes (directed edges, Table 1) are represented with no weight or differential location. When a non-circular representation (b) is allowed, here with an appropriate display algorithm (Kamada & Kawai, 1989), certain variables and processes become more central (here, termite workers *Wk*) and others less central (here, competitors *Ac*). The dashed ellipse highlights a possible definition of the ecosystem boundary of this termite ecosystem, on the basis of semi-characterized components (i.e., influencing but not influenced in turn by the system). This representation (b) of the ecosystem is not yet precise.

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Furthermore, it follows from this observation that every node, as a component, is a super-graph (made up of finer sub-nodes) in itself. Indeed, it is always possible, and sometimes relevant, to subdivide a population node into individuals or groups (e.g., population stages, age-wise, sex-wise), and to

177 emphasize their various actions, at various levels of organization. All these representations need to be
178 useful for the question being addressed, though, as it is often pointless to subdivide a component into a
179 new subgraph to achieve a more detailed representation of the system. This remains valid for a specific
180 interaction which it is pointless to subdivide into several (dyadic) processes. Whenever it is relevant for
181 the question being addressed to zoom in (to “unfold”) and/or zoom out (“fold”) part of the single graph
182 under examination, it is possible to split nodes into sub-nodes connected to other nodes already present
183 with distinct processes (Gaucherel, 2019; Montiglio et al., 2020). Such a procedure obviously requires
184 caution as it quickly encompasses distinct levels of organization (or scales) too.

185

186 **From graph to hypergraph**

187 In real systems, most variables are connected to many others, such as the aforementioned scientist
188 who interacts with other scientists for the purpose of communication, with salads as food and with
189 producers for shopping, through the processes of talking, eating and buying. Conversely, most processes
190 involve many components (variables) simultaneously, such as the communication process requiring the
191 scientist, potentially an organism under examination (the salad), and the audience. This observation
192 remains valid for any subgraph and discipline such as, for example, a physicochemical graph of chemical
193 reactions requiring reactants and catalyzers (Fontana & Buss, 1994; Cumming et al., 2014; Fages et al.,
194 2018). For these reasons, most interactions are called non-dyadic (i.e., not reduced to dyadic
195 interactions), a point that has been made recently for ecological networks too (Werner & Peacor, 2003;
196 Golubski et al., 2016; Delmas et al., 2018). In ecology and elsewhere, it may be that such non-dyadic
197 interactions are the norm rather than the exception. This leads to complex ENs with a large number of
198 complex interactions, which require appropriate concepts for disentangling them. Computer science has
199 developed conceptual and technical tools to handle such non-dyadic interactions and compute their
200 dynamic consequences. Known as *hypergraphs*, a number of associated tools have been developed to
201 handle them (e.g., Reisig, 2013; Battiston et al., 2020), although they remain somewhat limited,
202 especially for non-specialist practitioners, as compared to traditional dyadic graphs.

203

204 A *hypergraph* is a generalization of a graph in which edges, called *hyperedges*, may have several
205 incoming and outgoing nodes. In ecology, any variable may be connected through many processes and,
206 above all, any process may connect many variables, as in the case of the termite colony (Table 1). In our
207 studies, we use hypergraphs by dictating that nodes are the material components of social-ecological
208 systems and that edges are the abstract processes involving these components (e.g., Mao et al., 2021;
209 Cosme et al., 2022). Hence, any hypergraph is a means of representing the state of the ecosystem via the
210 composition of its components, while still considering their associated interactions. In addition, it is
211 possible to define the processes involved on the basis of equations or rules that represent the
212 components' interactions. Such process definitions, be they dyadic or not, naturally direct the associated
213 EN hyperedges in most environmental studies. Any hypergraph may be represented by a Petri net,
214 among other convenient tools developed in computer science (Fig. 3b). Petri nets were developed in the
215 1930s for modeling chemical reactions requiring precisely such connections and have since been used in
216 many other fields (Pommereau, 2010; Reisig, 2013; Pommereau et al., 2022b). In such a representation,
217 variables are known as *places* (round-shaped nodes) and interact through processes called *transitions*
218 (square-shaped nodes), shown as arcs. Any hyperedge may be represented by the set of arcs (or
219 *hyperarcs*) of a Petri net, connecting the nodes as the pre-condition and other nodes as the post-
220 condition of the focal transition (Fig. 3b). Petri net arcs may be weighted, and places may be multi-
221 valued, holding varied numbers of tokens, thus constraining their flows in the Petri net. Such bipartite
222 graphs are equivalent to hypergraphs as they allow an arbitrary number of nodes to be connected to an
223 arbitrary number of edges and vice versa (e.g., the termite colony EN, Fig. 3c).

224 Shifting to the termite hypergraph, we define specific symbols to signify the Boolean nature of each
225 node (component) in the rule (process) (Fig. 3a-b). Circular nodes are variables and represent social-
226 ecological components. A node is drawn with double lines if it is initially present in the system (Boolean
227 value +), or a single line otherwise (-). When a variable is present, its node has a token (not shown),
228 otherwise it does not. Square-shaped nodes are transitions and represent social-ecological processes.
229 Each process is defined graphically by a condition, arcs (round-tipped arrows, Fig. 3b), a transition node
230 and a consequence, and forms a directed hyperedge. A transition node “reads” and “writes” the values
231 (tokens) of variables. When an incoming arc (from a variable node to a transition node) has a black (resp.
232 white) dot, then the transition node “expects” the variable to have a token, i.e., to be present (resp.
233 absent). Conversely, when an outgoing arc (from transition node to variable) has a black (resp. white)
234 dot, then the action activates (resp. inactivates) the variable. In the Petri net, a variable activation (resp.
235 inactivation) corresponds to token production (resp. consumption). A variable may be present in the
236 condition and in the consequence of the same action. In this case, there will be a dot at each end of the
237 arc connecting the action to the variable. The resulting graph (Fig. 3c) unambiguously represents the
238 termite ecosystem EN, and thus explicitly links network structure and dynamics.

239 An example of non-dyadic interaction may be found in the last process (R9): $Ac^+, Sd^- \gg Wk^-, Rp^-$;
240 stating that termite workers (Wk) and reproductives (Rp) may both die when competitors (Ac) attack the
241 termite colony in the absence of soldiers (Sd) to defend it. Using the model’s terminology, the condition
242 “presence of competitors and absence of soldiers” enables and triggers the consequence “absence of
243 workers and reproductives”. In this case, a traditional graph representation (Fig. 3a) is not appropriate, as
244 it hides the exact connections of this four-node interaction. To be rigorous and to retain all the
245 ecosystemic information, we need a graph that explicitly shows which variables interact with each other,
246 and how. Inspired by Petri net notations, we propose to replace hyper-arcs (initially connecting nodes)
247 with another node type (like transitions in Petri nets, Fig. 3b). The resulting graph (Fig. 3c) unambiguously
248 represents the termite ecosystem EN (Fig. 2b), and thus explicitly links network structure and its potential
249 dynamics.

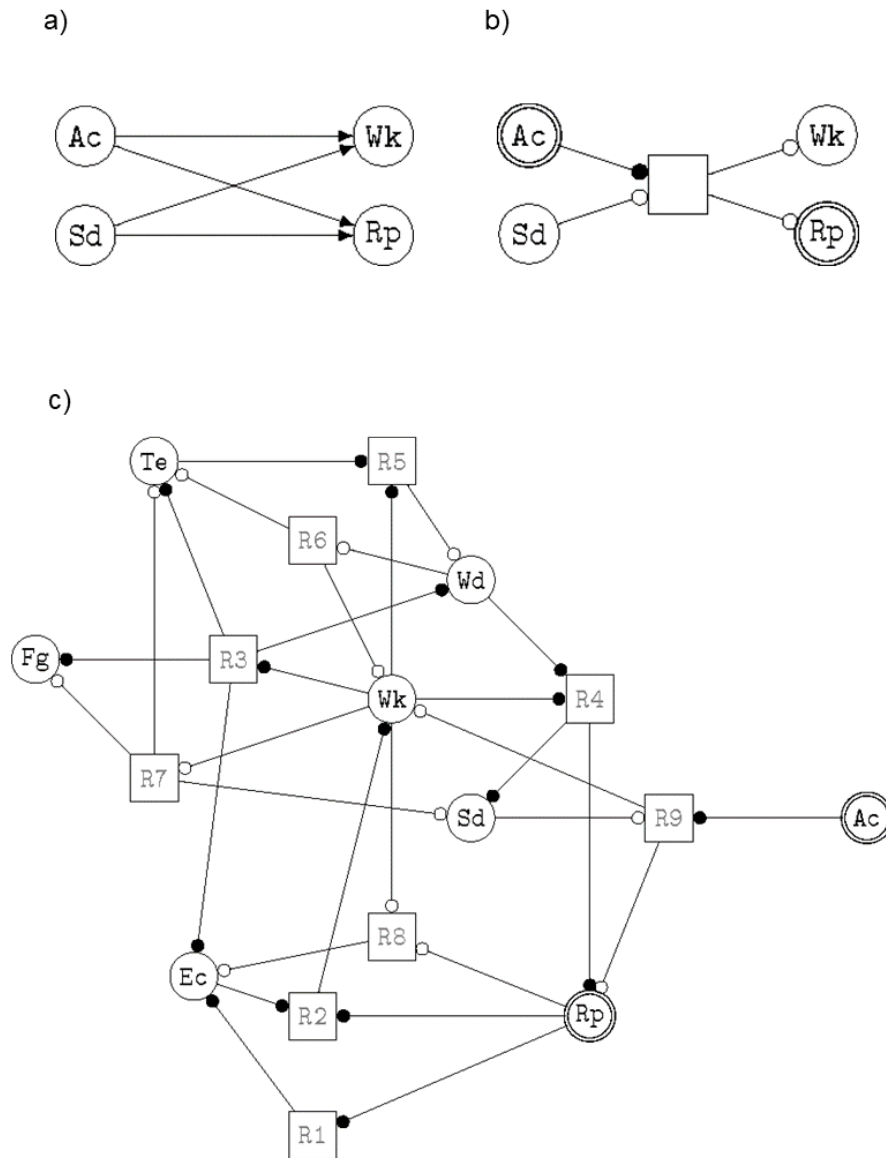


Figure 3

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Figure 3 - Illustrations of the symbols chosen here to accurately represent the ecosystem network hypergraph (a) and the full representation of the termite hypergraph (b, the same ecosystem as in Fig. 1). The sub-hypergraph corresponding to the last rule (R9) of the termite ecosystem (Table 1) is displayed: $Ac, Sd \rightarrow Wk, Rp$ with its corresponding traditional graph (a) and our proposed hypergraph notation (b). See the main text and (Pommereau et al., 2022a, 2022b) for explanations of each symbol indicating how tokens should circulate in the hypernetwork. The full ecosystem network hypergraph of the termite colony is displayed (c) with the corresponding symbols (b), and with the variable and process names found in Table 1.

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Simultaneously, it becomes relevant to analyze the EN structure itself and to highlight the graph topology for ecological insights (Fig. 2b-3b). Here, no shape is assumed for the EN; instead, the graph topology is allowed to emerge from the chosen variables and known interactions, bringing interacting variables closer and moving non-interacting variables further out. With an appropriate graph layout (Fig.

263 2b), algorithms and graph analyses (Kamada & Kawai, 1989), it is possible to produce representations
 264 that help in understanding node properties (e.g., whether they influence or are influenced by other
 265 nodes) and many other properties (e.g., betweenness, connectivity index) as is already routinely the case
 266 in ecology (e.g., Urban & Keitt, 2001; Foltête & Giraudoux, 2012). For example, a relevant *boundary* of
 267 the ecosystem under examination may be computed by excluding nodes that influence others but are not
 268 influenced in turn (e.g., the sun and other so-called *control variables*), and including all the others (e.g., a
 269 species simultaneously eating and being eaten) (dashed ellipse, Fig. 2b).

270

271 Qualitative ecosystem dynamics

272 Graphs and hypergraphs are by definition discrete. However, the interaction network they represent
 273 might not be (Dicks et al., 2002; Landi et al., 2018; Valverde et al., 2020), as their nodes may represent
 274 continuous variables and their edges continuous flows between them (Fig. 1a). In this paper, we propose
 275 to approximate the interaction network of any ecosystem with a qualitative hypergraph (still generically
 276 denoted as ‘EN’ hereafter). This hypergraph carries information about the potential qualitative dynamics
 277 of components, namely their appearance and disappearance (Fig. 1b). This description is relevant for
 278 long-term dynamics, as an observer who waits long enough will no longer measure flows and
 279 abundances, but appearance and disappearance of system components (and processes). In this spirit, we
 280 define a system component as a *Boolean* variable, i.e. having two discrete values, describing the
 281 functional presence/absence of the component in the system. A component that is functionally present is
 282 considered to pass a predefined threshold, present in most non-linear processes (R. Thomas, 1973), and
 283 to be able to influence (or be influenced by and possibly, no more influence) other components (Fig. 1b).
 284 Conversely, a process (potentially generating an *event*) is defined as a discrete change in the values of
 285 certain variables (the consequence) triggered by other variables (the condition). According to Petri net
 286 formalism (Pommereau, 2010; Pommereau et al., 2022b), these events are represented by *rules* written
 287 as “condition >> consequence” (Table 1). The change in one (or more) variable(s) is called a transition,
 288 which creates a new system *state*.

289 **Table 1** - List of the eight termite colony variables with their acronyms, initial states (+ or – beside
 290 each variable) and descriptions (columns 1 and 2), and the ten termite colony processes with their
 291 descriptions (columns 3 and 4). Simplified from the initial publications (Gaucherel et al., 2017;
 292 Gaucherel & Pommereau, 2019; Gaucherel et al., 2020).

<u>inhabitants:</u>	Descriptions	<u>rules:</u>	Descriptions
Rp+:	Reproductives	R1: Rp+ >> Ec+	Reproductives lay eggs
Wk-:	Workers	R2: Rp+, Ec+ >> Wk+	Eggs grow into workers
Sd-:	Soldiers	R3: Wk+ >> Wd+, Te+, Fg+, Ec+	Workers collect wood resource and maintain termitomyces and their gardens
Te-:	Termitomyces	R4: Wk+, Wd+ >> Sd+, Rp+	Workers and resources supply soldiers and maintain reproductives
<u>(spatial) structures:</u>		R5: Wk+, Te+ >> Wd-	Workers and termitomyces consume wood resources
Ec-:	Egg chambers	R6: Wd- >> Wk-, Te-	Without wood resources, workers and termitomyces die
Fg-:	Fungal gardens	R7: Wk- >> Fg-, Te-, Sd-	Without workers, fungal gardens (and thus termitomyces) and soldiers disappear
<u>Resources and competitors:</u>		R8: Wk-, Rp- >> Ec-	Without workers and reproductives, eggs cannot be laid
Wd-:	Wood	R9: Ac+, Sd- >> Wk-, Rp-	When competitors attack the termite colony without soldiers, workers and reproductives die

Ac+:

Ant competitors

293

294 The sequences of states and transitions are the system *dynamics*. The dynamics of a qualitative EN
295 would enable the sharp changes in the long-term dynamics of the ecosystem to be understood. In a way,
296 the single qualitative EN constitutes the *skeleton*, a kind of backbone of the (social-)ecological system
297 under study, intentionally neglects subtle variations and flows (Gaucherel & Pommereau, 2019; Cosme et
298 al., 2022), i.e., the component dynamics, and enables the computing of qualitative ecosystem dynamics,
299 the network dynamics (Gaucherel et al., 2017; Gaucherel, 2019). An EN hosts the tangled dynamics of
300 species abundances and other components and of flows between them. Many studies have developed
301 powerful models to simulate and understand such dynamics in networks with frozen topology (Thébault
302 & Fontaine, 2010; S. Kéfi et al., 2015). Using discrete-event models, it becomes possible to model
303 changing networks and their discrete dynamics (i.e., state and transitions). A system state is defined by
304 the values of all the variables. In the graph, a system state corresponds to a given token distribution
305 (called the *marking* in Petri nets) among the nodes (Fig 4a). A state transition occurs when the marking
306 changes, that is to say, when one or more tokens are produced and/or consumed in the graph.

307 Starting from an initial state (blue hexagon in Fig 4a, and column 1 in Table 1), the graph enables the
308 computation of all reachable system states and transitions (following green and pink states). The
309 modelled system may then bifurcate in state n°4 by following rule R1 (“Reproductives lay eggs”, Table 1)
310 or in state n°14 by following rule R9 (“workers and reproductives die”), and so on. These states and
311 transitions are usually represented as a State-Transition Graph (STG, Fig. 4a) (Berthomieu et al., 2004;
312 Reising, 2013). In this STG, any cycle (i.e., a set of mutually reachable states, also called structural
313 stabilities) or fixed state (a state with no outgoing transition, also called deadlocks) becomes now
314 identifiable and informative (Gaucherel & Pommereau, 2019; Gaucherel et al., 2020) (colors in Fig. 4a).
315 Hence, it is possible to automatically compute the discrete-event dynamics of the system from the
316 hypergraph structure (Fig 4b).

317

318 This is precisely what we modeled in several studies from a chosen EN of temperate and tropical
319 social-ecological systems (Mao et al., 2021; Cosme et al., 2022). By using specific tools, it is also possible
320 to formalize specific questions about the dynamics displayed in the STG, without explicitly computing
321 them, a relevant advantage when it becomes too large to be fully computed (Fages et al., 2004; Largouët
322 et al., 2012; C. Thomas et al., 2022). In addition to an intelligible visualization of ecosystem structure and
323 dynamics, we now have the benefit of the whole toolbox associated with such representations (Fig. 4b),
324 as with the Petri nets that computer science has developed (Berthomieu et al., 2004; Rodríguez &
325 Schwoon, 2013; Pommereau et al., 2022b). The demonstration of the relevance and application of Petri
326 nets and related concepts is outside the scope of this conceptual paper, but interested readers may refer
327 to recent papers (e.g., Gaucherel & Pommereau, 2019; Mao et al., 2021; Cosme et al., 2022). Such
328 models automatically produce STGs comparable to those already developed in many empirical ecological
329 studies (Stringham et al., 2003; Bestelmeyer et al., 2017). Looking ahead, several computing tools are
330 even able to automatically detect various kinds of topological structures and regularities/invariants
331 directly within the EN (Rodríguez & Schwoon, 2013; C. Thomas et al., 2022). For example, in theory,
332 individuals or populations that may exhibit cycles or that may collapse could be detected by such
333 invariants directly within the EN representation (Fig. 4b). This view supports an innovative conceptual
334 representation of the ecosystem.

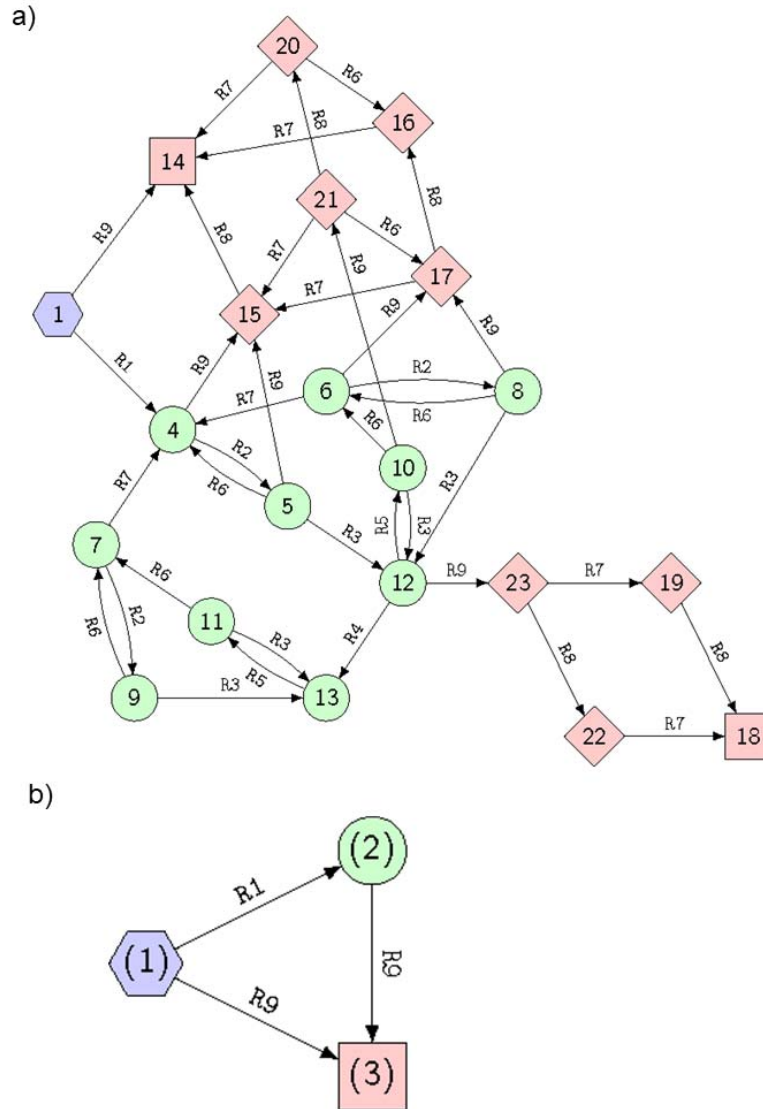


Figure 4

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Figure 4 - The termite ecosystem state spaces (or STGs), full (a) and merged (b), i.e., the dynamics computed from its corresponding ecosystem network hypergraph (Gaucherel & Pommereau, 2019; Pommereau et al., 2022a). The pathways start from the initial state (hexagon), follow various states according to process rules (defined in Table 1), cycle into sets of states (colors), and finally reach deadlocks (squares). The node labels are arbitrary identifiers of each state (a) and of each structural stability (in brackets, b), while each edge is labeled by the rule (Table 1) responsible for the system change.

343 A changing (and spatial) hypergraph

344 Disregarding for a moment variable abundances and process flows, this EN is in no way frozen. In the
345 long term, each component and each process potentially disappears and (re)appears in line with the
346 presence/absence of its material components (Fig. 1b). They can enter (e.g., species invasions or
347 pollutants) and/or leave (species extinctions or migrations) the system being studied. Our aim is to model

348 network dynamics, i.e., a changing topology, not to be confused with the dynamics of components in a
349 static network (i.e., flows “carried” by the frozen graph). In the long term, the nodes and edges of the
350 graphical representation themselves become fragile and ephemeral, depending on the other connected
351 variables, what previous studies have called *ecosystem development* (Gaucherel et al., 2017; Gaucherel,
352 2018). Conversely, in short-term dynamics with a similar level of detail, the EN retains the same structure
353 (Fig. 1 or any state in Fig 4a). This assumption of a fixed topology is still widely used in most ecological
354 studies today (e.g., Proulx et al., 2005; Golubski et al., 2016; S Kéfi et al., 2016). We posit that such
355 topological changes, or ecosystem development, strongly differ in nature to ecosystem *functioning*. We
356 developed a number of models and tools to analyze such qualitative dynamics. In the termite colony toy-
357 model, the STG computed from the chosen initial state is well suited to detecting stabilities, collapses,
358 and tipping points (Fig. 4b) in ecosystem pathways (Gaucherel et al., 2020), if any. Today, we are applying
359 this framework to large and more realistic observed social-ecological systems (e.g., Cosme et al., 2022;
360 Cosme et al., 2023), sometimes made up of dozens of components and hundreds of interactions of
361 contrasting nature.

362 In the long term, the (qualitative) EN topology is continuously changing, and these structural (or
363 network) dynamics may be largely disconnected from short-term component dynamics. Any sharp
364 change in the system will change the network topology, which is modeled by the token flow. Modeling
365 such a changing topology is highly difficult, however, because it implies anticipating any disappearance
366 and (above all) appearance of components. Practically, it is easier to initially assume the *maximal* EN
367 topology by including all possible components, and then mimicking their possible disappearance by
368 removing their associated nodes and/or tokens. For example, in our past studies, we model structural
369 changes in the EN representing the appearance and disappearance of components by changing the
370 Boolean values of their associated variables and nodes (Fig. 1b). This is known as the EDEN (for Ecological
371 and Social Discrete-Event Network) framework (Gaucherel & Pommereau, 2019; Pommereau et al.,
372 2022a). Such changes are generated by certain rules representing system processes and their related
373 transition events. The STG precisely computes the successive topologies of the EN, considering the
374 present and absent components and processes of the termite colony (nodes in Fig. 4a). Hence, any STG
375 state displays a distinct EN topology, mimicked by the variable changing states (Fig. 3). This makes the EN
376 an ever-changing hypergraph whose topology needs to be reconstructed for an understanding of the
377 long-term dynamics.

378 The EN representation does not fit with the traditional interaction networks in ecology or
379 environmental sciences as, firstly, we proposed to collect all the interaction networks present in an
380 ecosystem via qualitative approximation (Fig. 2); and secondly, as we proposed rigorous conventions for
381 this representation (Fig. 3), inspired by Petri nets which are well adapted for handling such mathematical
382 objects (Pommereau, 2010; Rodríguez & Schwoon, 2013). It is striking that most models used in ecology
383 today (mainly ordinary differential equation systems) are not appropriate for handling dynamic systems
384 on dynamic structures (called DS², Giavitto, 2003). Here, the central idea was to integrate all relevant
385 interactions for the question being addressed into the same graph, and to study the coarse (topological)
386 graph dynamics.

387
388 The EN is a coherent and convenient concept for summarizing all ecosystem components, whatever
389 their nature and complex interactions. It provides a way to achieve the often sought and rarely attained
390 integration of social-ecological systems (Ostrom, 2009; Mao et al., 2021). Another advantage of
391 qualitative ENs is their intelligibility (Dambacher et al., 2003; Thébault & Fontaine, 2010), even at larger
392 sizes, while quantitative models generally require a numerical analysis and act like black boxes. It is
393 possible to define extensions of the notation presented above that would use as many tokens as required
394 to model quantitative variations for each (multi-valued) variable, but at the cost of an explosion in STG

395 sizes and in the model's computation. And nothing prevents, then, the transformation of hypergraphs
396 into hybrid models combined with systems of differential equations for more quantitative analysis
397 (Samaga & Klamt, 2013). While most traditional models in ecology and environmental sciences are
398 limited to a dozen or so variables, with numerical computations, our qualitative models often handle
399 dozens of variables (Cosme et al., 2023).

400 In addition, the EN appears heuristic in that, in common with traditional interaction networks, it
401 reveals the ecosystem's internal structure: the EN topology collects internal variables and their specific
402 interactions, while highlighting external variables too (Fig. 2b, dashed ellipse). Such external nodes are
403 control variables that influence (toward ecosystem centrality) without being influenced in turn. In other
404 words, the boundaries of the ecosystem or the "skin", become visible on the skeleton. Nonetheless, i) the
405 ecosystem boundary is not necessarily a spatial or specific (e.g., species-centered) boundary, rather than
406 a multidimensional functional boundary (Fig. 2b), and ii) the hypergraph representation is not hampered
407 by the boundary definition so often debated (Gignoux et al., 2011; Gaucherel, 2018). It naturally emerges
408 here from the processes listed in the model, and from the question being addressed. When conceived in
409 this way, it becomes obvious that the ecosystem does not conserve matter and energy, and is
410 thermodynamically open (Jorgensen, 2001; S. P.-V. Frontier, D. et al., 2008). Conversely, ecosystem
411 variables located in the center of the EN hypergraph (e.g., termite workers in Fig. 2b), interact with more
412 variables in more diversified ways. They do not play a higher role, but they are more closely related to
413 the question being addressed, as the modeler explicitly considers its possible impacts and influences on
414 the rest of the system. Yet, we warn the reader that it may be dangerous to formulate potentially naive
415 interpretations on the basis of a displayed structure only.

416

417 In parallel, providing another perspective, all the points discussed previously may be included in
418 spatially implicit or explicit ecosystem models. Indeed, space itself is easily represented as a graph: in the
419 case of a spatially explicit ecosystem, the localities involved are potentially represented as nodes or
420 (unfolded as) a set of nodes themselves, and may be either individualized or merged into the same EN.
421 Space has long been modeled in this way, as a graph with changing topologies (Burel & Baudry, 2003;
422 Gaucherel et al., 2012). Conceptually, there is nothing to prevent the merging of the spatial
423 representation in the graph with the more functional EN we have described here: whenever various
424 localities need to be described in the same extensive overall super-graph (Felipe-Lucia et al., 2021), their
425 own EN (but not their corresponding spatial node) may be merged with neighboring ENs too. Hence, each
426 ecosystem may be represented as a changing single hypergraph, including its spatial structure. Although
427 such a single hypernetwork would seem huge, it brings the conceptual advantage to provide a coherent
428 view of any (social-)ecological system, as already mentioned in previous theoretical discussions
429 (Gaucherel, 2019).

430

431

Conclusion

432 The so-called ecosystem hypernetwork (EN, i.e., the social-ecological interaction hypergraph) fits our
433 need for efficient representation of any complex ecosystem, and provides several additional advantages.
434 It summarizes the internal structure of the system, a kind of synthetic skeleton of the components and
435 processes involved. In this study, we highlighted three points, illustrated with specific Petri net models.
436 Firstly, it is possible to collect all the ecosystem's interactions into a single EN, regardless of their nature,
437 number and how they intertwine. This proposed representation still shows intentional limitations: for
438 example, in this representation, components never interact directly; here, interactions are always

439 connected to a process. Similarly, no process can impact directly another process without being
440 connected to a component. This single EN is possibly not unique, as ecosystem models are driven by a
441 research question, thus leading to various representations of the same system.

442 Secondly, the EN is modelled as a hypergraph, which represents non-dyadic interactions more
443 explicitly. Events and components defining the system can be represented as distinct nodes of a bipartite
444 graph, as in Petri nets or, in our case, a qualitative hypernetwork (Fig. 3). Thirdly, the EN representing any
445 ecosystem is dynamic, with a changing topology. We provided an example of a framework (EDEN)
446 computing qualitative ecosystem dynamics based on transitions producing/consuming tokens in the
447 hypergraph. This enables a State-Transition Graph to be computed, collecting all the ecosystem states
448 reachable from the initial state, according to predefined events. This provides a coherent and effective
449 overview of the dynamics of any ecosystem.

450

451

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452

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453

Data, scripts, code, and supplementary information availability

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455

456

Scripts and code are available online: No data were used in this study; the method sources are archived at <https://github.com/fpom/ecco> which is the engine as well as the (Jupyter platform) interface of the EDEN framework.

457

Conflict of interest disclosure

458

459

The authors declare that they comply with the PCI rule of having no financial conflicts of interest in relation to the content of the article.

460

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