

Predicting The Sign of Trophic Effects: Individual-Based Simulation Versus Loop Analysis

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Abstract

Food web research needs to be predictive in order to support decisions system-based conservation. In order to increase predictability and applicability, complexity needs to be reduced to simple and clear results. One question emerging frequently is whether certain perturbations (environmental effects or human impact) have positive or negative effects on natural ecosystems or their particular components. Yet, most of food web studies do not consider the sign of effects.

Here, we study 6 versions of the Kelian River (Borneo) food web, representing six study sites along the river. For each network, we study the sign of the effect of a perturbed trophic group i on each other j groups. We compare the outcome of the relatively complicated dynamical simulation model and the relatively simple loop analysis model. We compare these results for the 6 sites and also the 14 trophic groups. Finally, we see if sign-agreement and sign-determinacy depend on certain structural features (node centrality, interaction strength).

We found major differences between different modelling scenarios, with herbivore-detritivore fish behaving in the most consistent, while algae and particulate organic matter behaving in the least consistent way.

Introduction

In complex, multi-species ecosystems, a number of interactions connect various organisms. Predicting the community-wide effects of single-species perturbations is a challenge for both ecological research and systems-based management.

In complex ecological systems, the multiplicity of direct and indirect interactions make it uneasy to provide simple and clear predictions on the effect of single-node perturbations. The effects on other organisms and, generally, community response is the outcome of a number of interconnected pathways. Predicting whether the influence of organism i on organism j will be positive or negative is not easy, even without considering non-trophic effects and complicated functional responses. Also the experimental results on positive inter-specific interactions are quite recent [1, 2, 3]. Considering effect sign is critically important, for example, if positive feedback loops [4, 5] or mutualisms [6] are to be understood.

Network analysis offers various methods for predicting effect sign. Loop analysis [7, 8], mixed trophic impact [9, 10], signed topological importance [11, 12] and dynamical simulations [13] can be used but their relationship is not straightforward (i.e. whether they provide similar or complementary information). Yet, loop analysis has been used extensively together with topological network analysis (e.g.[14, 15, 16]).

Generally speaking, topological models provide fast and easy but not very realistic results from a quite static viewpoint. Sophisticated food web simulations provide more accurate results but need a lot of data and offer results that can be harder to interpret. Qualitative models, like loop analysis, are somewhere in between, trying to combine simplicity (without explicit dynamics) and reality (interaction sign considered).

In this paper, we study food webs at the level of individual nodes (trophic groups), interspecific interactions and whole networks. We compare (1) the results of loop analysis and dynamical simulations predicting the sign of effects following single-node perturbations. Beyond comparing these two methods themselves, we also compare (2) the 6 food web models as well as (3) the 14 trophic groups. Finally, (4) we investigate if there is an correlation between various structural properties and sign-agreement.

Data And Methods

Data

We used 6 versions of the Kelian River (Borneo) food web for our analysis (data from [17, 18]). This makes it possible to assess spatial variability within the ecosystem.

The food web is described for 6 different locations along the river [13, 19], based on extensive earlier field work [17, 18]. The 6 sites represent a gradient from a pristine rainforest to a human settlement. The pristine food web (site 1) contains 14 trophic groups and 2 additional groups appear only downstream, so the total number of trophic groups is 16 (see Table 1). Most of the groups represent living organisms (e.g. PRED: invertebrate predators) but there are some non-living groups as well (e.g. POM: settled and suspended

coarse and fine Particulate Organic Matter). The definition of the groups and the description of interactions among them are based on long-term, extensive field work [17, 18].

Table 1. The abbreviation for the 16 trophic groups composing the 6 food webs.

ALGA	green and blue-green algae
CARN	carnivorous fish
COLF	invertebrate collector-filterers
COLG	invertebrate collector-gatherers
DIAT	diatoms
FILA	filamentous bacteria
GRAZ	invertebrate grazers
HEDE	herbivore-detritivore fish
HERB	herbivorous fish
HUMW	human waste
LEAF	leaf litter
OMNI	omnivorous fish
POM	settled and suspended coarse and fine Particulate Organic Matter
PRED	invertebrate predators
SHRE	invertebrate shredders
TERR	terrestrial insects

Food web structure: topological importance

We quantified the topology of the food webs based on the topological importance (TI^n) index that considers direct and indirect effects spreading along pathways of up to n step. This approach quantifies both the centrality of nodes in networks (TI_i) and the strength of effects between node i and node j (TI_{ij}). It is important to note that the latter can be calculated also for binary networks of un-weighted links: strength is the pure consequence of topology [20, 21].

The centrality of species (trophic groups) in food webs seems to be a systemic property with important ecological correlates (e.g. body size, mobility, see: [22]). There is a number of topological indices quantifying centrality in networks and their relationship is increasingly understood [23]. Since we must deal with indirect effects in order to assess the combinations of positive and negative impacts, we use the TI index, explicitly considering the length of direct and indirect pathways in food webs [20]. We note that TI is an useful centrality measure out of the many, according to a recent study wherer machine learning identified the most predictive combinations of centrality indices [24]. In this paper, we used TI^3 , i.e. we considered indirect effects up to 3 steps. We performed these calculations in order to see whether there is structural basis of (constraints on) the sign-agreement (for nodes and networks) and sign-determinacy (for interactions and networks).

Loop Analysis

Loop analysis is a qualitative method, that uses signed digraphs to illustrate networks of interacting variables [7, 8]. This technique gives the opportunity to represent the structure of linkages of the variables and the patterns of their variations [25, 26]. Also, the qualitative models allow to examine the effect of non-biological variables on our system (such as gold mining, fishing etc.). This qualitative modeling approach provides a method that is useful where species and their natural history are well-known, but not quantified [27].

Signed digraphs are based on the generally accepted interactions between nodes (trophic groups). These interactions come from the previous trophic models in [13]. The figures show two types of connections: arrows (\rightarrow) for positive and circle-head links (-o) for negative effects. These links are originated from the coefficients of the community matrix [7]. The diagonal terms of the community matrices are self-effects on system variables, represented in signed digraphs as links connecting variables with themselves. These links are self-dampening (circle-headed) with self-limiting growth rate. For a simple prey-predator system, see Figure 1.

Using the qualitative modelling framework of loop analysis, one can analyze pathways and feedbacks in the system, making predictions about the response of variables to perturbations. These can be the addition (increased biomass) or deletion (decreased biomass) of other nodes. Based on feedbacks and pathways, one can qualitatively specify the direction of changes. If we analyse relatively small systems (with $n < 5$ nodes), this can be executed through the direct analysis of the signed digraph. For larger networks, the graphical feedback analysis is difficult but one can calculate response predictions from mathematical operations on the community matrix.

We followed the method described in [26] to get the predictions for our networks. The loop formula is used for calculating the equilibrium value of the variables following a perturbation, so it can be deduced how does the abundance of a certain variable change [28]:

$$\frac{\partial x_j}{\partial c} = \frac{\sum_{i,k} \left[\frac{\partial f_i}{\partial c} \right] \times [p_{ji}^{(k)}] \times [F_{n-k}^{(comp)}]}{F_n} \quad (1)$$

On the left side, x_j is the variable with the equilibrium value being calculated and c is the changing parameter (e.g. mortality, fecundity, abundance). On the right side, f is the growth rate, $\partial f_i / \partial c$ designates whether the growth rate of the i^{th} variable is increasing or decreasing (positive or negative input, respectively), $p_{ji}^{(k)}$ is the pathway connecting the variable to the changed parameter (where the perturbation enters the system), $F_{n-k}^{(comp)}$ is the complementary feedback, which buffers or reverses the effects of the pathway and F_n designates the overall feedback of the system, which is a measure of the inertia of the whole system to change [26, 28]. See also [8] for the discussion of the correspondence between matrix algebra and loop analysis.

The net effect (the sum of the direct and indirect effects) on variable i resulting from a perturbation on variable j is given by the j - i^{th} element of the inverse community matrix $[A]^{-1}$. The sign of the coefficients of $[A]^{-1}$ give the direction of the expected changes for the variables [26]. To make predictions, we used a routine that randomly assigns numerical values from an uniform distribution to the coefficients of the community matrix (these coefficients belongs to the links of the signed digraph). This was performed $100 * N^2$ times, where N is the number of variables in the system. Matrices satisfying the asymptotic Lyapunov criteria were accepted and inverted. The routine of [26] calculated predictions for the probabilities based on the percentage of positive and negative signs and zeroes in the inverted matrices. They defined a set of rules to make a final table of predictions only from signs (Table 2, [26]).

Table 2. The frequency of positive („+“) effects in the inverted matrices defines the sign of predictions.

% of “+”	sign
0-24	-
25-39	?-
40-59	0*
60-74	?+
75-100	+
% of “0”=100	0

Half of the effects correspond to clear predictions (lower 25% for negative and top 25% for positive prediction). Less than a third of the effects correspond to weak predictions (15-15% for both weak negative and weak positive predictions). The fifth of the effects (the middle 20%) correspond to net zero prediction (“0“). Finally, „0“ means no change in the abundance of the variable [26].*

Community matrices show the links between the trophic groups. The elements in the rows affect the elements in the columns and the values could be -1, 0 or 1. These represent prey-predator (resource-consumer) effects. We decided to work with self-dampening variables only for living groups (see Table 3 for the community matrix of site 1).

Table 3. Community matrix for site 1.

	ALGA	CARN	COLF	COLG	DIAT	GRAZ	HEDE	HERB	LEAF	OMNI	POM	PRED	SHRE	TERR
ALGA	-1	0	0	0	0	1	1	1	0	1	0	0	0	0
CARN	0	-1	-1	-1	0	-1	-1	-1	0	-1	0	-1	-1	-1
COLF	0	1	-1	0	0	0	0	0	0	1	-1	1	0	0
COLG	0	1	0	-1	0	0	0	0	0	1	-1	1	0	0
DIAT	0	0	0	0	-1	1	1	1	0	1	0	0	0	0
GRAZ	-1	1	0	0	-1	-1	0	0	0	1	-1	1	0	0
HEDE	-1	1	0	0	-1	0	-1	0	-1	0	-1	0	0	0
HERB	-1	1	0	0	-1	0	0	-1	0	0	-1	0	0	0
LEAF	0	0	0	0	0	0	1	0	0	0	0	0	1	0
OMNI	-1	1	-1	-1	-1	-1	0	0	0	-1	-1	-1	-1	-1
POM	0	0	1	1	0	1	1	1	0	1	0	0	0	0
PRED	0	1	-1	-1	0	-1	0	0	0	1	0	-1	-1	0
SHRE	0	1	0	0	0	0	0	0	-1	1	0	1	-1	0
TERR	0	1	0	0	0	0	0	0	0	1	0	0	0	0

Direct trophic interactions are represented in such a way that the elements in the rows affect the elements in the columns and the values could be -1, 0 or 1, depending on field data. We decided to work with self-dampening variables only for living groups.

We were interested in the effect of decreasing the biomass of each trophic group (i.e. the value of each variable), one by one. For this, we needed to simply reverse our predictions [29]. By predicting these changes, qualitative models can also predict the correlation patterns between the examined groups/variables [8, 26, 28].

Levins' loop algorithm was extended in [29] to complex ecological systems. The adjoint of the negative of this community matrix shows the net number of complementary feedback cycles. A complementary feedback appears if k variables in the path are ideally excluded from the graph: what remains is called the complementary subsystem. The complementary feedback is the feedback that groups all the variables in the complementary subsystem [26] that contribute to the responses of other variables in the whole system. Therefore, the adjoint of the $-A$ is equivalent to Levins' loop analysis algorithm and its relation with the inverse matrix (A^{-1}) is:

$$-A^{-1} = \frac{\text{adjoint}(-A)}{\text{determinant}(-A)} \quad (2)$$

where the adjoint and inverse matrices are calculated with the negative of the community matrix, thus the positive input is read down the columns and the responses along the rows [29].

An „absolute feedback” matrix was defined in [29] to calculate the absolute number of complementary feedback cycles in a response whether positive or negative:

$$T_{ij} = \text{permanent}(\text{minor } A_{ij})^T \quad (3)$$

Where A denotes the adjacency matrix (absolute values of A).

The „weighted-predictions” matrix can be calculated from the Eq. (1)-(2):

$$W = \frac{\overrightarrow{|adj^{\circ}A|}}{T} \quad (4)$$

where „ \rightarrow ” is a vectorised matrix operator, what denotes element-by-element division ($W_{ij}=1$, when $T_{ij}=0$). The elements of W show the probability of sign determinacy of response predictions in the adjoint matrix. If all of them are of the same sign in one cell, then $W_{ij}=1$. If there is an equal number of negative and positive feedback cycles, then $W_{ij}=0$ [29]. The $W_{ij}=0.5$ value is a threshold for sign determinacy in models of any size [27].

Our values in the „weighted predictions” matrix were mostly under $W_{ij}=0.5$. According to this, most of the prediction signs were indeterminate. We used the adjoint values to investigate if sign determinacy depends on the strength of interactions (based on both structure and simulations).

Dynamical simulations

For the dynamical simulation data on the food webs, we used earlier results of an individual-based model [13, 19]. This simulation model was built in a process algebra-based framework [30]: abundance was calculated for the trophic groups and interaction strength was converted to probability, according to the kinetics of the stochastic simulation framework used routinely in systems biology [31, 32, 33, 34].

The stochastic IBM simulation model, set up with the parameters described in the field, was balanced by a genetic algorithm. Following the reference runs, sensitivity analysis was performed. The abundance of each trophic group was perturbed and the response of each other trophic group was measured. Since this was a stochastic model, both the mean and the variability were evaluated.

In this paper, we used only the sign of the responses (not their strength). For comparability, minimal changes must be made in the results of the dynamical simulations: since these categories do not exist in simulations, ?+, ?- and 0* predictions were considered as +, - and 0, respectively. Further, as the effects in dynamical simulations never result exactly in 0, we needed to define zero effects during the simulations. We decided to have the same number of zeroes in the simulation results as we got in the predictions of loop analysis. Values in this „corridor” of the smallest positive and negative simulation outcomes were considered 0.

Software

We used MASS 7.3-51.5 and nlme 3.1-148 R packages for the analyses. For simulating sign predictions, we used the R code in [26]. The LoopAnalyst 1.2-6 package was used for the calculations of the adjoint of the $-^{\circ}A$ and the “weighted predictions” matrices (and it required the nlme package, too). Figure 3-4 were created with GVEdit Graph File Editor For Graphvizversion: 1.02 Graphviz version:2.38.

Statistical methods

Sign-agreement was examined on several levels. We compared the predictions of loop analysis to the calculations made by the structural importance index TI^3 and to the results of dynamical simulations for the whole networks, for individual nodes (i.e. the rows of the matrices) and for individual interactions.

As described above, we categorized the outcome of dynamical simulation results into 3 categories (+, 0, -). This way, the table of predictions from loop analysis and the matrix of simulation effects became comparable (both containing only +, - and 0). A binary sign-agreement matrix contained 1 (yes) for similar and 0 (no) for different signs in the two matrices. The percentage of 1 values served for quantifying sign-agreement (1s in the main diagonal, corresponding to self-effects, were not considered).

Chi-square tests were applied for the effect signs for each node, determining if there is significant difference in either loop analysis or dynamical simulations.

In order to see if there is some structural basis for sign-determinacy and sign-agreement, we tested the correlation between (1) the adjoint matrix and the dynamic simulation results, (2) the adjoint matrix and interaction strength calculated by TI_{ij} , (3) the dynamic

simulation results and interaction strength calculated by Tl_{ij} and (4) sign prediction of loop analysis and node centrality measured by Tl_j .

Results

Figure 2 shows the food web for each of the 6 sites. The number of trophic groups varies between 12 and 15, starting from 14 in the pristine forest (site 1).

The predicted sign of effects for each trophic group is shown in Figure 3, for each of the 6 sites (Figure 3a – 3f). In site 1 (Figure 3a), mutually negative (CARN-HEDE), mutually positive (CARN-OMNI), antagonistic (LEAF-GRAZ) uni-directional positive (TERR-PRED) and uni-directional negative (HERB-CARN) interactions can be seen. Between some pairs of trophic groups, there is no interaction predicted (e.g. CARN and COLG). Higher sign-agreement is seen for organisms at higher trophic levels. This pattern seems to be the same also for site 2 (Figure 3b) but not for the other sites. Site 4 (Figure 3d) is simpler than the previous sites, with some groups having only a single interaction partner (e.g. CARN, HEDE, COLG). The differences among the sites are quite characteristic in loop analysis, while the simulation models vary less. Site 6 (Figure 3f) is strongly dominated by factors essentially external to the stream ecosystem (TERR and HUMW).

Sign-agreement predicted by loop analysis and by the dynamic simulations are shown in Table 4, at the level of the whole networks and for individual nodes (this latter is represented by the colours in Figure 3: sign-agreement increases from light yellow to dark green). The mean correspondence of signs at the network level is under 50 %. Maximum sign-agreement ranged between 50 and 64.29% and the minimum was between 7.14 and 27.27%. On average, site 6 in the Kelian River is the ecosystem where loop analysis best predicts the signs of dynamical simulation results. From site 2 to site 6, there is a monotonous increase in mean (and the minimal) sign-agreement (the maximum values show no trend and also site 1 is out of this pattern). This suggests that the two methods provide different, complementary information on the ecosystem. Some organisms generally give consistent behaviour (e.g. HEDE), while others (ALGA, POM) behave differently in different modelling environments. Whether POM will have positive or negative impact on others is differently predicted in 5 out of 6 sites.

Table 4. Sign-agreement (between predictions of loop analysis and results of dynamical simulations) for nodes and networks.

	Network min	Network mean	Network max	Node min	Node max
site 1	23.08	38.46	61.54	ALGA, COLF, POM, PRED	HEDE
site 2	7.69	28.57	61.54	ALGA, COLG, POM, SHRE	HEDE
site 3	14.29	32.86	50	SHRE	HEDE, CARN
site 4	18.18	36.36	54.55	ALGA, POM, OMNI	COLG, DIAT
site 5	21.43	38.1	64.29	ALGA, COLG, COLF, POM, TERR	PRED
site 6	27.27	45.45	63.64	POM	TERR

Mean, minimum and maximum values characterize whole matrices. The trophic groups with minimum (least predictable) and maximum (most predictable) values are shown.

Sign-agreement was measured also at the level of individual interactions. The mean of sign-agreement is also under 50% but the maximums are between 50-72% (Table 5). The high sign-agreement for HEDE is seen also in the interactions in this group, being involved in 4 out of 7 of the highest-agreement interactions. It is also noted that the same group (HEDE) can be involved in minimum (HEDE-POM) and maximum (HEDE-TERR) agreement interactions (see site 2). It is noted that COLG in site 5 has several minimal-agreement interactions (e.g. COLG-POM), after being the most predictable group in site 4 (with the most predictable interaction, COLG-CARN).

Table 5. Sign-agreement (between predictions of loop analysis and results of dynamical simulations) for interactions.

	Network min	Network mean	Network max	Interaction min	Interaction max
site 1	19.23	35.71	65.38	ALGA-HERB, ALGA-SHRE, COLF-PRED, POM-CARN, POM-GRAZ	HEDE-COLF
site 2	3.85	26.53	50	POM-HEDE	HEDE-ALGA, HEDE-TERR
site 3	7.14	30.67	57.14	COLF-FILA	HEDE-SHRE
site 4	13.64	33.33	68.18	ALGA-HEDE, OMNI-HEDE, OMNI-TERR, POM-HEDE, POM-TERR	COLG-CARN
site 5	17.86	35.56	57.14	ALGA-COLG, CARN-COLG, COLF-COLG, POM-COLG, TERR-COLG	PRED-LEAF
site 6	18.18	41.67	68.18	FILA-OMNI, POM-HERB	TERR-CARN

Mean, minimum and maximum values characterize whole matrices. The inter-specific interactions (direct and indirect effects) with minimum (least predictable) and maximum (most predictable) values are shown.

The Chi-square tests showed that the predictions of loop analysis for different trophic groups were significantly different only for site 4 of Kelian River (Figure 4a, see Appendix A for all of the other simulations), while the Chi-square tests for the results of dynamic simulations did not show significant differences (Figure 4b). Based on loop analysis (Figure 4a), CARN, COLG and HEDE have predominantly zero and occasionally positive effects on others. On the contrary, TERR (and to some extent POM) have the highest proportion of negative effects. Dynamical simulations (Figure 4b) show a different outcome with DIAT being the only one without negative effects and HEDE (and ALGA) with the largest negative impacts. According to Appendix A, there are significant differences among the distribution of impact signs of various organisms in almost no cases. In some cases, this homogeneity is quite strong (e.g. site 3, loop analysis with 3 categories), while there are models with non-significant but visible differences (e.g. GRAZ and HEDE in the simulation model of site 2). In the model of site 4, loop analysis with 5 sign categories also provided significant differences among the organisms: the pattern is qualitatively similar to the result of the model with 3 sign categories (see Figure 4).

Spearman correlation ($|\rho|$ values) suggest no strong correlations between our values. Only the structural interaction strength (T_{ij}) and the adjoint values (LA_{adj}) showed significant correlation in site 4 of the model (see Appendix B).

Conclusions

Predictive food web research would be a quantitative and holistic toolkit for systems-based conservation efforts. Good predictions on strong and weak as well as positive and negative effects are important for management and policy. While dynamical simulation exercises require a large number of parameters and complicated models, the semi-quantitative methodology of loop analysis offers simpler and faster results, generally easier to understand and interpret. Structural analyses are the simplest and least realistic ones. The major question was to what extent simpler methods can replace the more complicated ones.

Comparing the sites, we see that the relatively consistent predictability of HEDE is seen in the sites of otherwise contrasting signs (site 2, site 3). The most consistent interaction happens between TERR and CARN in the most consistent model of site 6. This is the case when loop analysis and the dynamical simulation model mostly agree on sign prediction.

Based on Table 4, the general pattern emerges that higher sign-agreement is characteristic for trophic groups at higher trophic levels in sites 1-3, while trophic groups at lower trophic levels in sites 4-6.

Supposing that both models are relevant and correct, the question emerges why and to what extent should they be similar to each other. Similarity means that one reinforces the other, while differences may suggest that they are complementary, providing different kind of information. In the future, mixed trophic impact analysis, signed topological importance and further kinds of dynamical simulations must also be compared to the models studied here.

It is a question if experimental studies (e.g. mesocosm experiments) could help to better understand the predictability of effect signs and their differences in different modelling environments. Performing experiments only for a few species (e.g. perturbing COLG) might

help a lot in calibrating the amount of expected changes and scale the models.

It needs to be better understand how trophic complexity is related to predictability, in terms of either interaction strengths or interaction signs. Earlier research, based on time series data, found quite convincing results on the dimensionality of niche space [35].

Future research can be extended, for example, towards (1) considering the asymmetry of interactions (MEPS) and (2) considering loop sign [36, 37]. The former could be important in order to better understand cause-effect relationships, as strong asymmetry may imply causality. The latter could help to better assess network-level stability.

Abbreviations

ALGA: green and blue-green algae

CARN: carnivorous fish

COLF: invertebrate collector-filterers

COLG: invertebrate collector-gatherers

DIAT: diatoms

FILA: filamentous bacteria

GRAZ: invertebrate grazers

HEDE: herbivore-detritivore fish

HERB: herbivorous fish

HUMW: human waste

LEAF: leaf litter

OMNI: omnivorous fish

POM: settled and suspended coarse and fine Particulate Organic Matter

PRED: invertebrate predators

SHRE: invertebrate shredders

TERR: terrestrial insects

Declarations

Ethics approval and consent to participate

Not applicable

Consent for publication

Not applicable

Availability of data and materials

The datasets used and/or analysed during the current study are available from the corresponding author on reasonable request.

Competing interests

The authors declare that they have no competing interests.

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Authors' contributions

V.F. performed the loop analysis modeling and the statistical analysis. She wrote the paper.

F.J. framed the research idea, coordinated the project and wrote the paper.

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Figures

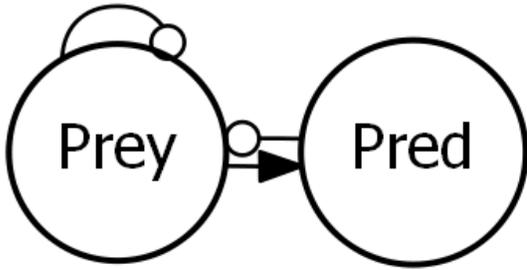


Figure 1

Signed digraph of a simple prey-predator system. The prey affects positively the predator („Pred“), indicated by a black arrow. Empty circles indicate negative effects: from the predator to the prey and the self-effect of the prey.

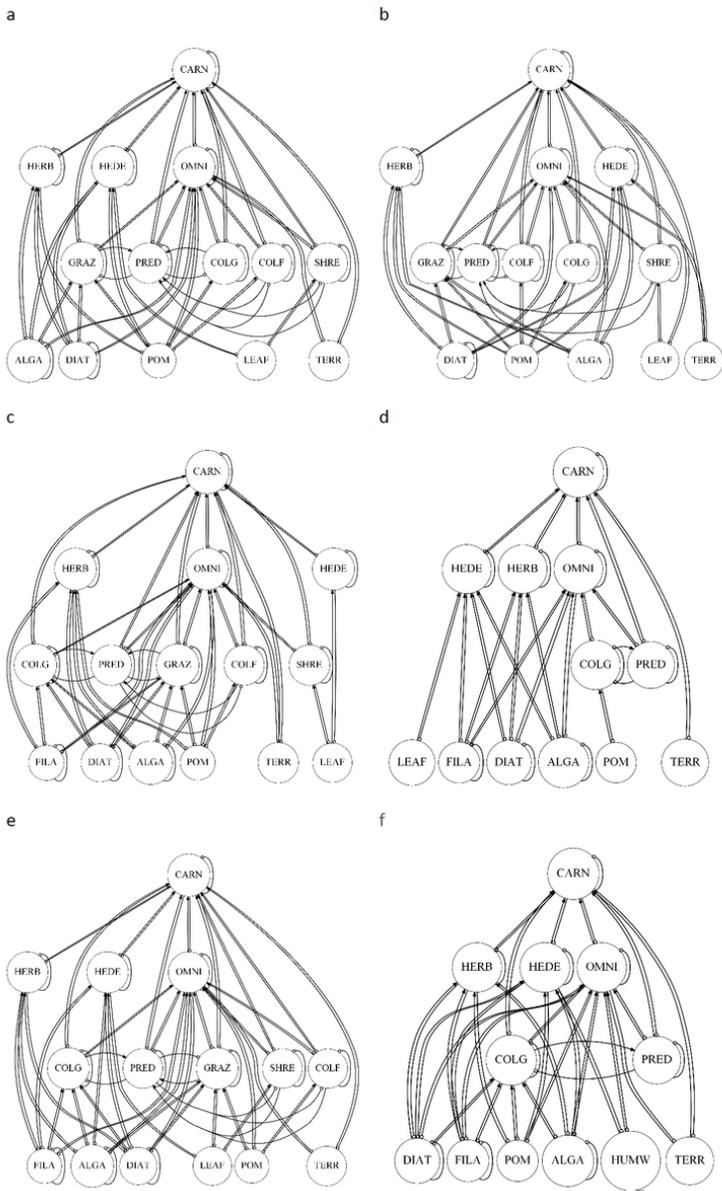


Figure 2

Food web of the Kelian River ecosystem in sites 1-6 (a-f). The arrow shows the consumer and the circle shows the resource for each trophic flow (who eats whom). Trophic groups are arranged according to trophic height.

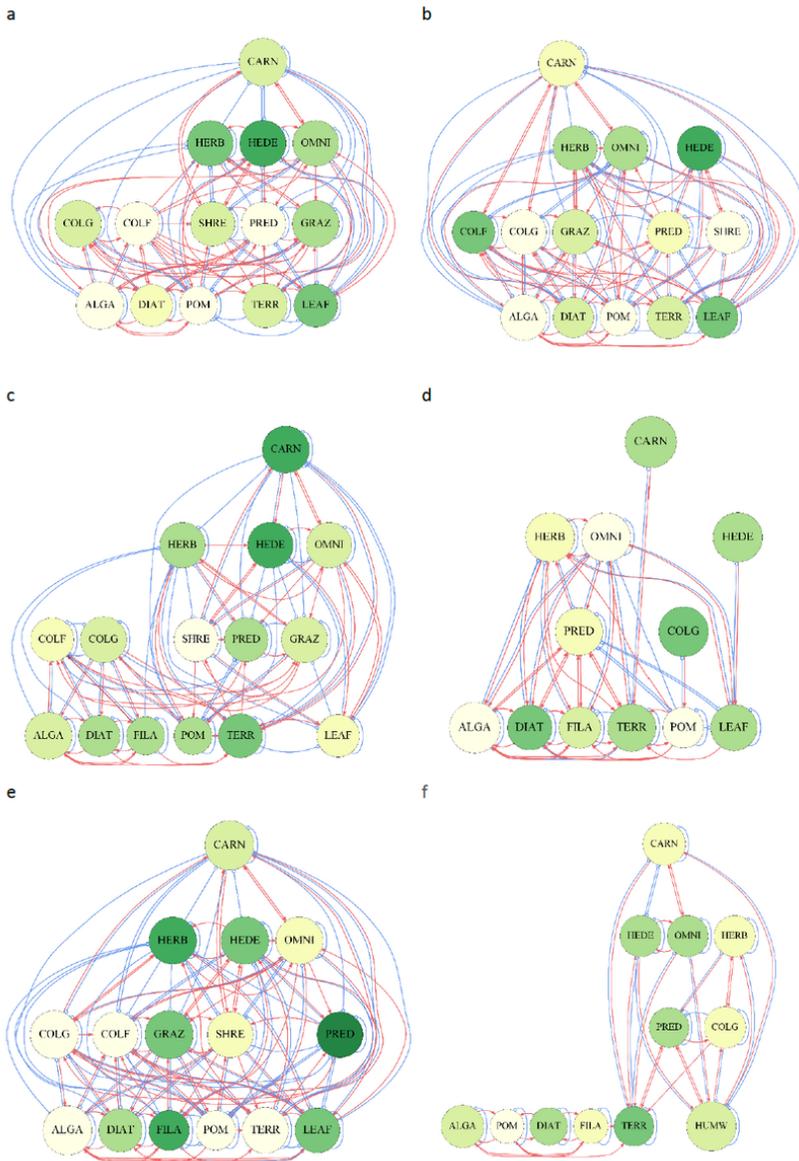


Figure 3

Food web of the Kelian River ecosystem in sites 1-6 (a-f). Arrows show the predictions of loop analysis: the sign of the effect of decreasing the abundance of a node on another (red is positive, blue is negative). The colour of nodes shows sign-agreement (%) between the predictions of loop analysis and the results of dynamical simulations (increasing from light yellow to dark green). Whether perturbing the light yellow nodes has positive or negative effect on others largely depends on the model chosen (see Table X). On the contrary, the perturbation of dark green nodes is similarly predicted by both approaches (see Table X). Colored by ColorBrewer [38].

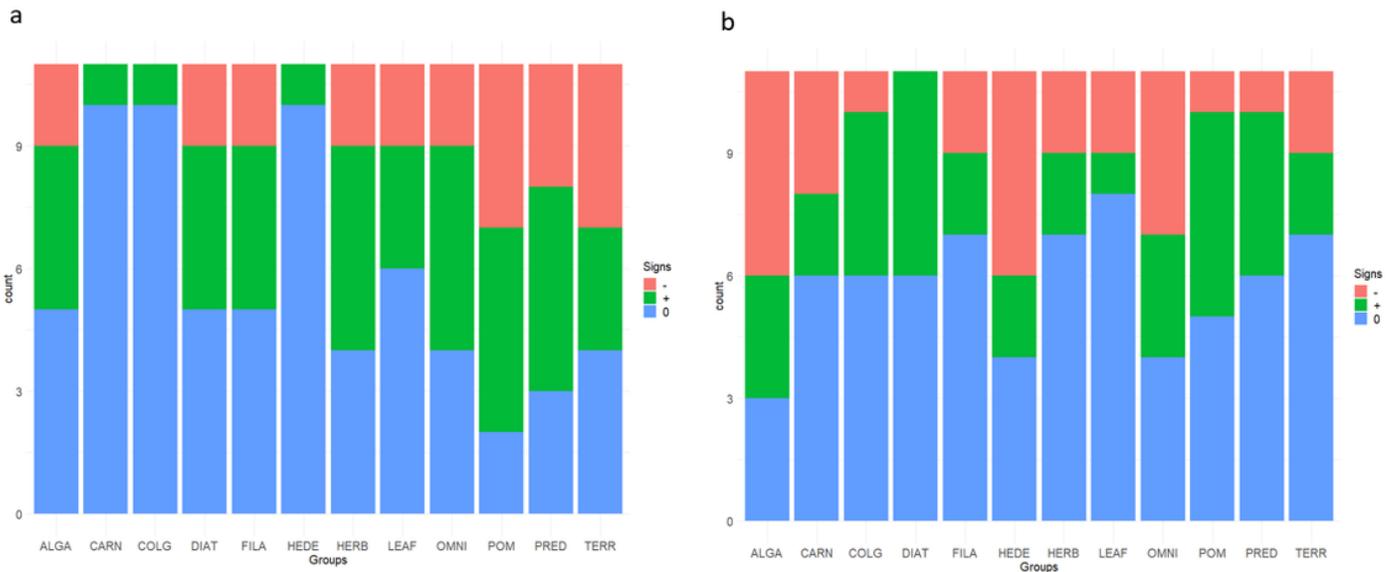


Figure 4

The number of positive (green), negative (red) and zero (blue) effects. Each 14 functional group are listed along the x axis, and the 13 other are counted along the y axis. This figure represents site 4 of the Kelian River ecosystem model, based on loop analysis (a) and dynamical simulations (b). In order to make them comparable, the predictions of loop analysis were transformed: we used only 3 categories, +? was replaced by +, -? was replaced by - and 0* was replaced by 0. The sign composition of organisms differs significantly in (a) ($\chi^2_{222}=34,67$; $p=0,04193$) but not in (b) ($\chi^2_{222}=22,989$; $p=0,4024$). The same plots for other ecosystem models as well as the plots for loop analysis with 6 prediction categories are shown in Appendix A.

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- [AppendixA.xlsx](#)
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