Maintaining the productivity of co-culture systems in the face of environmental change

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Co-culture systems can address food security issues by sustainably intensifying production of crops and animal protein without requiring additional land area. We show how a graph-theoretic optimization model based on ecological network analysis can determine robust co-culture strategies by controlling the presence of key species. Results of simulations on a hybrid rice and crayfish production system indicate that comparable levels of productivity can be achieved with different ecological network structures.

Feeding the world’s population within sustainable land, water and nutrient footprints is a daunting challenge. Climate change further threatens the capacity of food production systems to keep pace with growing demand. Aquaculture of lower-trophic-level species may provide a larger share of future protein requirements; however, the production of feeds for, and generation of organic pollutants from, intensive aquaculture raise sustainability concerns. Hybrid agriculture/aquaculture or co-culture can intensify food production while alleviating environmental footprints by using ecological engineering principles. For example, rice cultivation provides opportunities for the co-culture of aquatic animals in paddy fields, often based on non-optimal traditional farming practices or on conventional agronomic field studies. Ecological network analysis (ENA) can be useful for understanding interactions among wild and domesticated organisms within co-culture systems. ENA methods such as the static Ecopath model are based on linear systems of equations that reflect trophic mass and energy balances. They are widely used for ecosystem management for their ability to describe complex interactions among species. However, such models are rarely used for optimization and are generally limited to describing the state of ecological networks.

Descriptive ENA models are not sufficient for ecological engineering, which entails the design of systems with specific desired characteristics such as productivity or robustness. Ecological network optimization (ENO) techniques are needed to fill this research gap. We develop a new approach for the identification of productive co-culture systems using a socio-ecological process graph model, which captures how components in a defined ecosystem interact among themselves and with society. This modelling approach is an extension of process graph methodology to ENA, with ecosystems being treated as production systems to meet the needs of human consumers. The current model focuses on the demand pull of human consumption on the network, without considering feedback loops or dynamics; the effect of human interaction with the ecosystem will be dealt with in our future work. This application requires a prescriptive, rather than descriptive, model. The process graph method was originally developed for engineering design but has been applied to a broad range of analogous problems. The socio-ecological process graph is a bipartite graph that uses two disjoint sets of nodes to represent ecosystem components (O-type ‘ecosystem functional unit’ nodes represented by horizontal bars) and their functions (M-type ‘ecosystem service’ nodes represented by circles); this distinction allows a single species to be represented fully if it plays multiple roles in an ecosystem. No two nodes within the same set of the graph are connected by an arc. Three component algorithms are then used to generate and optimize network structures (Methods). To illustrate the additional insights that can be drawn from our technique, we use the rice–crayfish co-culture farming system (Supplementary Fig. 1) modelled elsewhere. That model was developed and validated using the state-of-the-art in Ecopath methodology considering both plausibility and data fit. The farm system consists of 13 different species interacting in a food web. The socio-ecological process graph is used to perform a combinatorically complete search of ecological interactions to generate candidate structurally feasible networks. The resulting structures can serve as a skeletal framework for subsequent detailed analysis that considers the magnitudes of the flows and interactions. The search algorithms use constraints that include mass balances and the existence of known ecological interactions. The search domain for finding feasible ecological interactions in the ecosystem can be reduced by eliminating or replacing species without losing any ecological interactions. The details of this ENO approach are described in Methods.

The co-culture system simultaneously produces rice and crayfish using the same land area without an external supply of supplements. The diverse ecosystem embedded in this farm includes aquatic plants, phytoplankton, benthic animals and zooplankton. The purpose of the modelling is to identify robust optimal networks that maximize the system productivity per unit land area; if the co-culture system is designed to maintain the yield of the primary crop, the productivity can also be measured in terms of the crayfish–rice ratio. We also assume that the crayfish has a flexible diet. Selected interactions among functional groups or species are illustrated in the Supplementary Information. Simulations were performed to maximize crayfish production per unit of rice. Solving the model generates 60 alternative optimal and near-optimal solutions from a maximal structure that contains all possible network linkages (Supplementary Information). Differences in productivity result from varying distribution of nutrients within these structures. Figure 1 shows the structure that provides optimal harvest or production of 80.23×10−2 kg of crayfish per kg of rice (Supplementary Table 1). The optimal harvest can be obtained with fixed/assumed supply of aquatic plants, rice, phytoplankton and detritus as food sources for crayfish (Fig. 1a,c). The network is much sparser than the maximal one, whose structure can be seen in the greyed-out parts of the figure (or see Supplementary Fig. 1). Comparing the optimal structure to the other top 14 structures enumerated in

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Fig. 1 | Optimal rice–crayfish co-culture system. a, c, Conventional schematic diagram where broken lines signify crayfish outputs (a) and socio-ecological process graph (c) of the co-culture system. The socio-ecological process graph consists of O-type nodes (bars) and M-type nodes (dots) linked by arcs (arrows) that signify trophic relationships; the grayed out parts of the graph indicate species not present in this particular network. The numbers next to the nodes are just numerical labels. b, Comparison of the optimal ecosystem (structure 1) to the other top 14 structures, showing that aquatic plants, rice, phytoplankton and detritus are the identified food sources of crayfish. The 15 solution structures in b are biologically different ecosystems with similar productivity (their respective socio-ecological process graphs are presented in the Supplementary Information).
Fig. 1b, it is clear that the productivity of a given network depends not just on which species are present but on how they interact in the food web.

Figure 2 shows the trends with changing ecosystem structure against the number of species present and productivity based on the mass of crayfish per unit of rice, the latter being a proxy for land area. The key result is that there are families of ecosystem structures that differ in the number and type of biological species but have nearly identical productivity. For example, structures 1 to 4 have similar levels (~0.12 kg of crayfish per kg of rice) but the number of species sequentially varies from five to nine. All 60 structures contain crayfish, plants, rice, phytoplankton and detritus, with structures 1 and 4 having only these five species. Structure 2 includes rotifer, bacteria and bacterioplankton and structure 3 additionally has cladocera. These are biologically different ecosystems with similar productivity. Note that there are several sequences or families of structures where productivity is robust and varies minimally if the species present significantly change. These 15 solution structures are shown in more detail in the Supplementary Information.

For the family of structures 5 to 15, the productivity varies from 0.095 kg kg⁻¹ to 0.097 kg kg⁻¹, or about 20% lower than the optimal solution, while the number and type of species varies from four to ten. All the ecosystem structures include crayfish, plants, rice and phytoplankton. Different combinations of the other species are present in these solutions. The biological functions of the missing species are taken by the remaining species that occupy similar ecosystem niches. Note that structure 14 has the largest number of species and the most redundancy in this family.

Our results demonstrate how the analysis of alternative network structures can be used to ensure productive co-culture systems. Rather than identifying a unique (and possibly brittle) optimum, the process graph approach is used to identify families of solutions which translate into options that give good productivity while being robust to disruptions. These solutions provide guidance on the management of co-culture operations but, in practice, controlling species present will require further research work. Such information can be used to guide future agronomic co-culture field experiments by identifying potentially favourable system configurations (for example, ditch shape or surface area) and farming practices. This approach has general applicability to a wide range of networks beyond the co-culture systems examined here, including portfolio optimization of ‘poly-culture’ food production.

Methods
The socio-ecological process graph is a bipartite graph consisting of M-type nodes (circles) to represent ecosystem services and O-type nodes (horizontal bars) to represent ecosystem functional units. This modelling technique is intended for the analysis and optimization of ecosystems for provision of human needs and is based on a class of engineering design problems known as process network synthesis (PNS). Arcs indicate interactions between ecosystem services and ecosystem functional units. If the M-type node is linked to more than one O-type node, it can be produced interchangeably by any combination of the latter. Inputs to an O-type node indicate ecosystem services necessary for its survival. Some ecosystem services can be classified as exogenous (originating from outside the ecosystem) or terminal (exiting the ecosystem for human use). The latter may be regarded as the final product of the ecosystem. Ecosystem services that are produced and consumed entirely within the ecosystem network are classified as intermediates. In the special case where only trophic linkages are considered, this technique uses assumptions that are compatible with those of static Ecopath models.

We have the following core assumptions. SE1: All the terminal ecosystem services must be generated by the ecosystem solution structure. SE2: An ecosystem service represented in the structure is exogenous if, and only if, it is not an output of a functional unit defined in the ecosystem structure. SE3: Only those ecosystem functional units that are defined in the ecosystem can appear in an ecosystem solution structure. SE4: Any ecosystem functional unit has at least one path to a terminal ecosystem service. Every ecosystem functional unit contributes to the terminal ecosystem service. This assumption ensures that all functional units are non-redundant but are directly or indirectly involved in the generation of the final product. SE5: If an ecosystem service belongs to the ecosystem structure, it must be an input to or output from at least one ecosystem functional unit represented in the structure. In a socio-ecological process graph, the mass/energy is available to keep the ecosystem structure functioning and to meet the ecosystem services goal(s), such that a cost metric (for example, money or ecological footprint) is minimized.

The maximal structure generation (MSG) algorithm generates a network that is the union of all combinatorially feasible networks. The solution structure generation (SSG) algorithm is capable of generating all combinatorially feasible networks, on the basis of enumeration of possible structures arising from relationships between ecosystem services and ecosystem functional units. MSG and SSG focus on network connectivity and do not account for transfers between units. The accelerated branch-and-bound (ABB) algorithm is used to determine optimal and near-optimal structures by evaluation of the performance of candidate networks, while excluding infeasible and redundant networks. Unlike the conventional branch-and-bound algorithm used to solve generic mixed integer linear programming models, ABB uses inherent information embedded in all PNS problems to reduce the size of the search space during optimization. For more details, the reader may refer to a recent book on process graphs.

Reporting summary. Further information on research design is available in the Nature Research Reporting Summary linked to this article.

Data availability
Data used in the analysis can be obtained via https://github.com/EcologicalP-Graph/Optimal-rice-crayfish-co-culture-system-find/main.
Code availability
The software P-graph Studio (v.5.2.2.2) is hosted by the Department of Computer Science and Systems Technology at the University of Pannonia in Hungary. It is available free of charge for research purposes via www.p-graph.org. The current v.5.2.2.2 runs in Microsoft Windows. The following specifications are required: Microsoft.NET Framework 4.5.1 (x86 and x64) and Windows Installer 4.5. Interested readers can replicate or modify our results using the P-graph Studio model file accessible via https://github.com/EcologicalP-Graph/P-graph Studio model file accessible via https://github.com/EcologicalP-Graph/Installer 4.5. Interested readers can replicate or modify our results using the P-graph Studio model file accessible via https://github.com/EcologicalP-Graph/

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Author contributions
H. C. and R.R.T. conceived the study. K.B.A. developed the model. A.R.L. created the graphics. All authors analysed the data, wrote the article and did the revisions.

Competing interests
The authors declare no competing interests.

Additional information
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Our web collection on statistics for biologists contains articles on many of the points above.

Software and code

Policy information about availability of computer code

Data collection | Simulations were done using the software P-graph Studio (Version 5.2.2.2) developed by the Department of Computer Science and Systems Technology at the University of Pannonia in Hungary. It is available free of charge for research purposes via www.p-graph.org.

Data analysis | No software used.

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### Ecological, evolutionary & environmental sciences study design

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| Study description | Graph theoretic simulations were performed for a rice-crayfish co-culture system. |
|-------------------|----------------------------------------------------------------------------------|
| Research sample   | The dataset reported by Dong et al. ([https://doi.org/10.1016/j.aquaculture.2021.736626](https://doi.org/10.1016/j.aquaculture.2021.736626)) was used as basis for the simulations. |
| Sampling strategy | Not applicable to the nature of our work. |
| Data collection   | Data was generated via graph theoretic simulations as previously described. |
| Timing and spatial scale | Not applicable to the nature of our work. |
| Data exclusions   | All results of the simulations are reported. |
| Reproducibility  | All our simulations are perfectly reproducible with the model file and datasets which are available in a public repository. |
| Randomization     | Not applicable to the nature of our work. |
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