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Is ecosystem structure the target of concern in ecological effect assessments?

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ABSTRACT

The species sensitivity distribution, a technique currently used to derive water-quality standards of chemicals, is associated with a set of inadequately tested assumptions. One of these assumptions is that ecosystem structure is as or more sensitive than ecosystem function, i.e., that structure is the target of concern. In this paper, we tested this assumption for a simple freshwater ecosystem exposed to different toxicants. Using an ecosystem model, we calculated no observed effect concentrations (NOECs) for ecosystem structure (ecosystem structure-NOECs) and function (ecosystem function-NOECs) for each of 1000 hypothetical toxicants. For 979 of these toxicants, the ecosystem structure-NOEC was lower than or equal to the ecosystem function-NOEC, indicating that the tested assumption can be considered valid. For 239 of these 979 toxicants, both NOECs were equal. For half of the 1000 toxicants, the structure of lower trophic levels (i.e., phytoplankton) appears to be more sensitive than the structure of higher trophic levels (i.e., fish). As such, ecosystem structure-NOECs are primarily determined by the sensitivity of the structure of lower trophic levels. In contrast, ecosystem functions associated with higher trophic levels (e.g., total ingestion by fish) are more sensitive than functions associated with lower trophic levels (e.g., total photosynthesis by phytoplankton) for 749 toxicants.

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1. Introduction

In ecological effect assessments and water-quality standard setting, higher-level effects are usually estimated by extrapolation of single-species toxicity test results. If sufficient single-species toxicity test results are available, statistical models, termed ‘species sensitivity distributions’ (SSDs) are used to perform this extrapolation. A set of assumptions is associated with both the underlying theory (‘T-assumptions’) and the application of SSDs (‘P-assumptions’), as discussed in

detail by Forbes and Calow (2002). Several authors have examined these assumptions experimentally (e.g., Duboudin et al., 2004a; Hose and van den Brink, 2004; Versteeg et al., 1999). However, these efforts have been focused on testing the P-assumptions (e.g., Kefford et al., 2005; Maltby et al., 2005; Duboudin et al., 2004a; Forbes et al., 2001; Hose and van den Brink 2004), rather than on testing the T-assumptions (Selck et al., 2002; Balczon and Pratt, 1994). Yet, the underlying theory is of fundamental importance for the SSD concept. While the way in which SSDs are applied can be customized

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according to the specific effect assessment, the underlying T-assumptions cannot as they are an inherent part of the SSD concept. Indeed, proper application of a methodology may still result in incorrect evaluation of ecological effects if the theory underlying the methodology is invalid.

Crucial to the endurance of ecosystems is the maintenance of ecosystem functions, as reflected by the stability concept (e.g., Steiner et al., 2005). Ecological stability is referred to as the ability of a community to (1) maintain ecosystem functions (resistance) when exposed to a stressor, and (2) recover to control levels of functioning after disappearance of the stressor (resilience) (Mac Gillivray et al., 1995). As such, an effect on ecosystem functions may indicate a loss of stability, possibly threatening ecosystem endurance.

Although ecosystem function is generally considered less sensitive than ecosystem structure, theoretical ecology indicates that the opposite may also hold. On the one hand, ecosystem functions may be less sensitive than ecosystem structure because species performing an ecosystem function may be replaced by less sensitive species capable of maintaining the same function (i.e., functional redundancy) (Pratt and Cairns, 1996; van Leeuwen et al., 1996). This was experimentally confirmed by Selck et al. (2002) for tributyltin and linear alkylbenzene sulfonates. On the other hand, environmental contamination may act as a selective force against populations of sensitive species, resulting in the loss of these species and possible cascading effects on ecosystem function (Lawler et al., 2002). Although necessary (Chapman et al., 2003), an examination using a general hypothesis-testing framework has not been performed.

In this paper, the assumption that ecosystem function is less sensitive than ecosystem structure, hereafter termed 'assumption T3', was tested in a simple freshwater ecosystem exposed to different toxicants. The term 'ecosystem function' is understood as in Duffy (2002) and Schlapfer and Schmid (1999), i.e., as the transfer of energy, expressed as biomass flows. Examples are total primary production, secondary production, aggregate consumption, community respiration, and nutrient uptake. In this paper, we studied the sensitivity of the photosynthesis of phytoplankton, the ingestion by zooplankton, and the ingestion by fish. An ecosystem model was used to predict the no observed effect concentrations (NOECs) for those three functions in an ecosystem exposed to 1000 hypothetical toxicants. With the same model, also NOECs for changes in ecosystem structure, expressed as biomass, were calculated. This allowed to compare ecosystem function-NOECs with corresponding ecosystem structure-NOECs for each of the 1000 considered toxicants.

2. Materials and methods

2.1. Ecosystem type

The ecosystem for which hypothesis T3 was tested is a lentic pelagic freshwater system, consisting of populations of one fish species, three zooplankton species, and two phytoplankton species (Fig. 1). The ecosystem functions studied were total photosynthesis of phytoplankton ($PS_{\text{phyto},\text{tot}}; \text{mgL}^{-1} \text{d}^{-1}$), total ingestion by zooplankton ($I_{\text{zoo},\text{tot}}; \text{mgL}^{-1} \text{d}^{-1}$), and

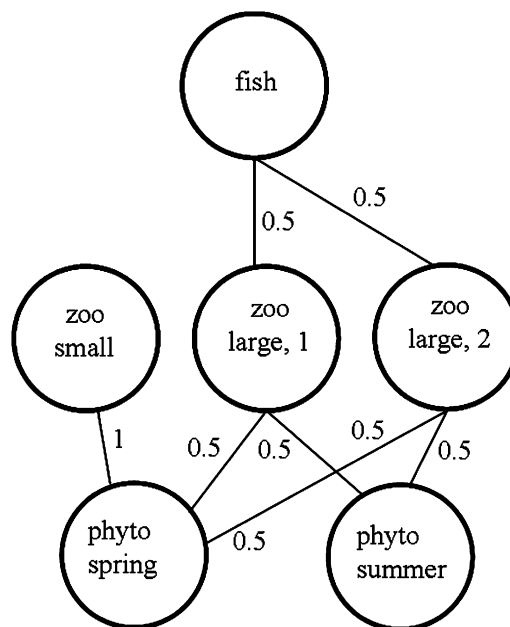


Fig. 1 – Food web diagram of the considered ecosystem. Nodes represent the populations present and lines represent feeding links between them. The preference of a population for a connected population is given by the preference factor alongside the connection. Zooplankton and phytoplankton are coded by 'zoo' and 'phyto'. 'Small' and 'large' indicate dimensions of zooplankton organisms. 'Spring' and 'summer' indicate when the considered phytoplankton population blooms.

ingestion by the one fish population ($I_{\text{fish}}; \text{mgL}^{-1} \text{d}^{-1}$):

$$PS_{\text{phyto},\text{tot}} = PS_{\text{phyto},\text{summer}} + PS_{\text{phyto},\text{spring}}, \quad (1)$$

$$I_{\text{zoo},\text{tot}} = I_{\text{zoo},\text{large}} + I_{\text{zoo},\text{small}},$$

with 'large' and 'small' indicating large, slow-growing and small, fast-growing populations, respectively, and 'summer' and 'spring' indicating populations blooming in summer and spring, respectively.

The choice to express ecosystem functions as fluxes of biomass was made because these are intuitively sensible, practical measures of energy assimilation (Johnson et al., 1996). Also, field studies tend to use some measure of biomass fluxes as the ecosystem function response variable (Johnson et al., 1996).

2.2. Ecosystem model

Effects of chemicals on the populations in the considered ecosystem were predicted using a methodology based on an ecosystem model that has been described previously (De Laender et al., 2007) and validated (De Laender et al., in press). A mechanistic dynamic ecosystem model was constructed using an object-oriented framework. The model consists of a set of objects, where each object describes the growth of a population in terms of its total biomass using differential

equations based on USEPA (2002). By connecting different objects and defining the trophic links between them, a customized food web can be designed. Additionally, the growth kinetics of these objects are differentiated by parameter tuning (slow-growing populations vs. fast-growing populations). A detailed overview of all model equations can be found in the supporting document. The ecosystem modelled in the present study included two phytoplankton objects (spring phytoplankton: small-celled and fast growing; and summer phytoplankton: large-celled and slow growing), three zooplankton objects (rotifers: fast growing; large cladocerans: slow growing; large copepods: slow growing), and one planktivorous fish object. Ecological interactions were set according to Sommer et al. (1986). Large-bodied zooplankton (most copepods and cladocerans) graze on both small and large phytoplankton, while small-bodied zooplankton can only ingest small phytoplankton. Planktivorous fish preferred large-bodied over small-bodied zooplankton as food source (Werner and Hall, 1974; Chang et al., 2004).

The ecosystem model was calibrated to obtain a realistic succession of seasonal events for this type of system, as described in Sommer et al. (1986). These events are (1) bloom of spring phytoplankton, (2) bloom of small zooplankton, resulting in a ‘clear water phase’, (3) a bloom of summer phytoplankton, followed by (4) a bloom of larger zooplankton, and (5) a small peak of fish. Parameter values resulting in population dynamics reflecting those events are given in the supporting document.

The toxic effect sub-models embedded in the ecosystem model consist of logistic concentration–effect functions describing the effects of the toxicants on the parameters of the ecosystem model. Modelling the dynamics of an exposed ecosystem is performed by adjusting these parameters according to the concentration–effect functions and the exposure concentration. Parameters in the ecosystem model, which vary as a function of toxicant concentration, are (1) the mortality rate of zooplankton and fish, and (2) the photosynthesis rate of phytoplankton. An overview of the equations of the toxic effect sub-models and the values assigned to their parameters is given in Table 1.

2.3. Structural vs. functional sensitivity for one hypothetical toxicant

Assume that for a toxicant tx_1 , all chronic single-species $EC_{10}S$ of all possible aquatic species are represented by a lognormal species sensitivity distribution SSD_1 :

$$SSD_1 \sim (\mu_1, \sigma_1).$$

From SSD_1 , six $EC_{10}S$ were randomly sampled to represent the single-species sensitivity of the six considered populations. These six $EC_{10}S$ were used in the toxic effect sub-models of the six populations in the ecosystem model. This allowed for the simulation of the dynamics of these populations at different exposure concentrations of tx_1 . Exposure concentrations ranged from the 1st to the 95th percentile range of SSD_1 . The exposure period was taken from late spring to late summer, which is comparable to many large-scale studies.

Changes in ecosystem structure were quantified by changes in biomass status of the populations. To compare the biomass status of a population in the unexposed (control) situation with its status at the different exposure concentrations, relative differences (RDs) were calculated:

$$RD_{tx,p} = \frac{X_{tx,p} - X_{ref,p}}{X_{ref,p}}, \tag{1}$$

where $X_{tx,p}$ is the time-averaged biomass concentration of population ‘p’, when exposed to a toxicant concentration ‘tx’; $X_{ref,p}$ the time-averaged biomass concentration of population ‘p’ in the unexposed case, i.e., the reference value.

Because 20% is the minimum detectable difference for most population characteristics in the field (Suter II, 1993), RD values of -0.2 or lower were considered as detectable decreases of biomass. Similarly, RD values of 0.2 or higher were considered as detectable increases of biomass. In the context of ecological effect assessments, both increases and decreases of phytoplankton biomass were considered undesirable. For fish and zooplankton, biomass decreases were considered as undesirable. The NOEC of a population, hereafter termed ‘population-NOEC’, was defined as the highest concentration at which no observable undesired effect was

Table 1 – Equations used in the toxic effect sub-models of the applied ecosystem model, with P_{max} = maximum photosynthesis rate ($d-1$); $P_{max,0}$ = intrinsic maximum photosynthetic rate ($d-1$); tox = toxicant concentration; EC_{50} , P_{max} = effect concentration for a 50% reduction in photosynthesis rate; slope = slope of the respective concentration–effect function; K_{mort} = mortality rate ($d-1$); \ln = natural logarithm; time = duration of toxicity assay (d), set to 2 days for all zooplankton and fish; LC_{50} = lethal concentration for 50% of the organisms, as determined in the acute toxicity assay; LCR = ratio of “lethal effect concentration” to “chronic effect concentration”

Phytoplankton: effect on photosynthesis	Zooplankton and fish: effect on mortality
$PS_{max} = \frac{PS_{max,0}}{1 + (tox/EC_{50,PS_{max}})^{slope}}$ $E_{50,PS_{max}} = \exp(\ln(EC_{10,PS_{max}})) - \frac{1}{slope} \cdot \ln\left(\frac{1}{9}\right)$	$Mort = \frac{1}{time} \cdot \ln\left(1 + \left(\frac{tox}{LC_{50}}\right)^{slope}\right)$ $\frac{LC}{EC_{10}} = LCR$
Values for LCR (6.1 for zooplankton and 9.5 for fish) were found in Lange et al (1998). Values for slope (1.8 for all populations) were found in Smit et al (2001). EC_{10} values were randomized (see methodology).	

predicted for that population. The NOEC of the ecosystem structure, hereafter termed 'ecosystem structure-NOEC', was defined as the lowest population-NOECs.

Similarly, the rate of an ecosystem function '*f*' in the unexposed (control) situation was compared with its rate at the different exposure concentrations by calculating relative differences. Also for these ecosystem functions, RD values of -0.2 or lower were considered as detectable decreases of ecosystem function rate. The highest concentration at which no detectable decrease of 20% or more on a considered ecosystem function occurred was defined as the ecosystem function-NOEC, allowing to rephrase hypothesis T3 as

ecosystem structure-NOEC \leq ecosystem function-NOEC.

2.4. Extension to 1000 hypothetical toxicants

The methodology described in the previous paragraph was followed for toxicants tx_1 – tx_{1000} . SSD_1 – SSD_{1000} differed in mean but, for reasons of feasibility, had the same default standard deviation ($\sigma_1 = \sigma_2 = \dots = \sigma_{1000} = 1$). A standard deviation of one order of magnitude is representative for SSDs of many chemicals (e.g., examples in Duboudin et al., 2004b). The means of the 1000 toxicants were sampled from a lognormal distribution with mean -0.43 and standard deviation 0.92 . These variability settings were found in Gonzalez-Doncel et al. (2006) from means and standard deviations of NOEC values of fish ($n = 343$), crustaceans ($n = 414$), and algae ($n = 186$) for all toxicants included in different toxicity databases.

In the next phase, we examined whether the type of toxicant could predict if ecosystem structure-NOEC was

smaller than or equal to the ecosystem function-NOEC. Toxicant type was arbitrarily defined here on the basis of relative sensitivities of the considered species to the toxicant. Relative sensitivities were defined by the following two quantities:

$$r_{PZ} = \log(EC_{10, \text{phytoplankton}}) - \log(EC_{10, \text{zooplankton}}), \quad (2)$$

$$r_{ZF} = \log(EC_{10, \text{zooplankton}}) - \log EC_{10, \text{fish}},$$

with $\log(EC_{10, \text{phytoplankton}})$ and $\log(EC_{10, \text{zooplankton}})$ equal to the logarithm of the geometric mean of the EC_{10} values of the two phytoplankton and three zooplankton species, respectively. A stepwise discriminant function analyses (Jennrich, 1977) was used to determine which variable (r_{PZ} and r_{ZF}) discriminates best between toxicants for which ecosystem structure-NOEC \leq ecosystem function-NOEC and those for which ecosystem structure-NOEC $>$ ecosystem function-NOEC. Partial lambda values were calculated for r_{PZ} and r_{ZF} , with a value of 0 indicating a perfect discriminative power, and 1 no discriminative power at all.

3. Results and discussion

3.1. Structural vs. functional sensitivity for hypothetical toxicants

For 979 of the 1000 toxicants, the ecosystem structure-NOEC was lower than or equal to the corresponding ecosystem function-NOEC (Fig. 2). As such, the tested assumption T3 appears to hold for the functions studied in this simple ecosystem. However, among these 979 toxicants, 239 had an ecosystem structure-NOEC equal to the corresponding

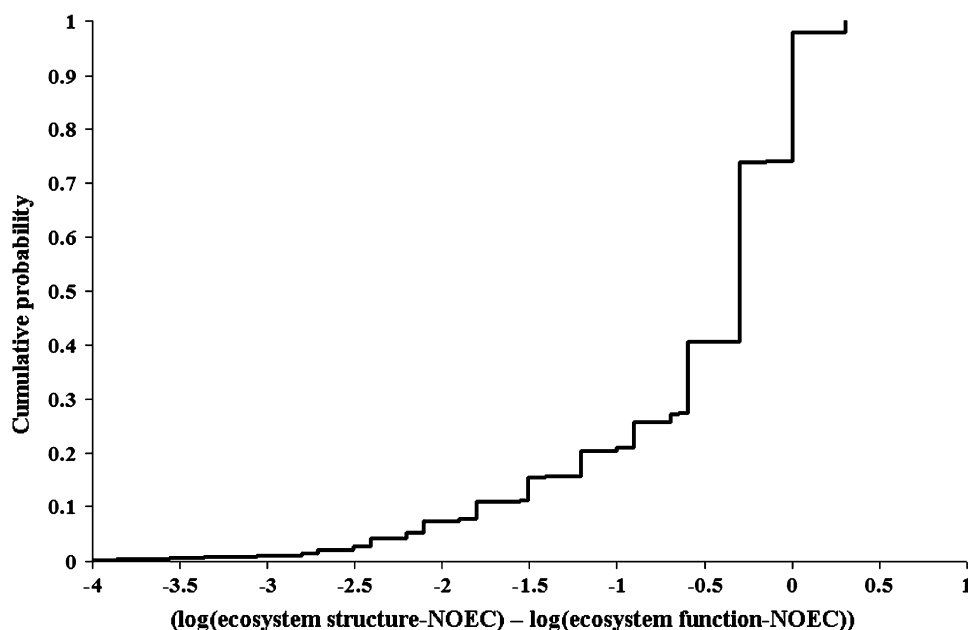


Fig. 2 – Cumulative probability distribution of the difference ($\log(\text{ecosystem structure-NOEC}) - \log(\text{ecosystem function-NOEC})$). Negative values indicate toxicants for which the ecosystem structure-NOEC was lower than the ecosystem function-NOEC. Values equal to '0' indicate toxicants for which the ecosystem structure-NOEC was equal to ecosystem function-NOEC.

ecosystem function-NOEC. Thus, for the latter toxicants a protection of structure is not necessarily a more conservative approach for the protection of ecosystem functions, but rather an accurate one. Based on the relationship of ecosystem resistance and resilience with ecosystem functions (Mac Gillivray et al., 1995), protection of structure seems crucial when this ecosystem is exposed to these 239 toxicants. Unfortunately, toxicant type could hardly distinguish toxicants for which ecosystem function-NOEC equals ecosystem structure-NOEC. A discriminant analysis showed limited power for r_{ZF} , as indicated by a partial lambda value of 0.86. The partial lambda value of r_{PZ} was 1, indicating no discriminative power at all for this variable. As such, determining *a priori* if ecosystem structure and function NOEC are equal, based on toxicant type alone, was not possible. Instead, one has a 23.9% probability of ecosystem structure being equally sensitive as ecosystem function when evaluating the ecological effect of a random toxicant.

In this paper, we defined toxicant type in terms of the effects a toxicant has on biological organisms of different trophic levels, i.e., on the substance's ecotoxicological properties. It should, however, be noted that the chemical properties of a substance can serve equally well to classify toxicants. In view of possible environmental concerns about substances of which only the structure is well known, it would be interesting to use the latter classification in future modelling exercises. Integrating the chemical definition of 'toxicant type' with its ecotoxicological definition would involve the incorporation of quantitative structure-activity relationships into the current study.

3.2. Which populations determine the ecosystem structure-NOEC?

For 467 of the 1000 toxicants, the most sensitive population, i.e., the one with the lowest population-NOEC, was a phytoplankton population. For 216 toxicants, this was a zooplankton population, while for only 64 toxicants this was the fish population. For the remaining 253 toxicants, populations from different trophic levels had the lowest population-NOEC. These calculations suggest that in the system studied, population-NOECs increase with increasing trophic level, regardless of the toxicant considered. Because it is defined as the lowest population-NOEC, the ecosystem structure-NOEC is determined by phytoplankton for 467 of the 1000 toxicants. In contrast, fish seem to play a role in the determination of the ecosystem structure-NOEC for only 64 of the 1000 toxicants. Because these findings are independent of the toxicant type considered, they only result from the ecological interactions included in the ecosystem model. As stated before, ecological interactions will lead to indirect effects on populations initially not targeted by the toxicant. A number of authors use the food web concept to explain how these indirect effects may occur (e.g., Relyea and Hoverman, 2006; Chapman et al., 2003; Fleeger et al., 2003; Preston and Snell, 2001). However, an extensive enumeration of possible indirect effects was not pursued here. Instead, the increase of population-NOECs with increasing trophic level was generally understood as an indication of dominant top-down regulation in this food web. Apparently, a change in a population's

biomass resulting from direct toxicant effects will affect the biomass of connected populations at lower trophic levels (i.e., indirect toxicant effect) more than it affects the biomass of connected populations at higher trophic levels. This finding agrees with indirect effects of toxicants observed in micro- and mesocosm studies (e.g., Relyea and Hoverman, 2006, Kneib, 1991; Posey and Ambrose, 1994; Menge, 1995; Brett and Goldman, 1996; Hay, 1997; Havens, 1995). Indeed, these authors have found that top-down-regulated indirect effects are more frequently observed than bottom-up-regulated indirect effects in experimental ecosystems exposed to toxicant stress.

3.3. Which functions determine the ecosystem function-NOEC?

For 749 toxicants, the ecosystem function with the lowest NOEC was I_{fish} , as such determining the ecosystem function-NOEC. This is confirmed by cumulatively plotting the NOECs of the three studied ecosystem functions (Fig. 3). A mechanistic explanation for this is that I_{fish} is the only function maintained by one single population (fish). In contrast, $I_{zoo,tot}$ and $PS_{phyto,tot}$ can be maintained by three and two populations, respectively. As such, the functional roles of these populations are redundant with respect to $I_{zoo,tot}$ and $PS_{phyto,tot}$, making those two ecosystem functions less sensitive. However, the relative sensitivity of ecosystem functions is not entirely explained by the number of populations maintaining it. The NOECs of $I_{zoo,tot}$, a function maintained by three populations (zoo_{small} and $zoo_{large,1}$ and $zoo_{large,2}$), appear to be lower than those of PS_{tot} , a function maintained by only two populations (phytoplankton_{small} and phytoplankton_{large}, Fig. 3). This suggests that ecosystem functions maintained by populations at higher trophic levels have a lower NOEC. At this point, we need to underline that ecosystem functions were defined as transfer rates of energy which are quantified by biomass, as is usually done (e.g., Duffy, 2002; Schlapfer and Schmid, 1999). Transfer rates associated with higher trophic levels are lower because of metabolic energy losses (Odum, 1971). Use of this concept reformulates the ecosystem functions studied as follows:

$$PS_{phyto,tot} = \eta_{Light} \rightarrow PS_{phyto,tot} \cdot Light, \tag{3}$$

$$\begin{aligned} I_{zoo,tot} &= \eta_{PS_{phyto,tot} \rightarrow I_{zoo,tot}} \cdot PS_{phyto,tot} \\ &= \eta_{PS_{phyto,tot} \rightarrow I_{zoo,tot}} \cdot \eta_{Light \rightarrow PS_{phyto,tot}} \cdot Light, \end{aligned}$$

$$\begin{aligned} I_{fish} &= \eta_{I_{zoo,tot} \rightarrow I_{fish}} \cdot I_{zoo,tot} \\ &= \eta_{I_{zoo,tot} \rightarrow I_{fish}} \cdot \eta_{PS_{phyto,tot} \rightarrow I_{zoo,tot}} \cdot \eta_{Light \rightarrow PS_{phyto,tot}} \cdot Light, \end{aligned}$$

with η representing the efficiency coefficient (<1), indicating energy (biomass) transfer efficiency between two transfers (functions). Names of ecosystem functions are as in Eq. (1). Toxicant effects on these ecosystem functions can be represented as follows:

$$PS'_{phyto,tot} = (1 - E_{PS_{phyto,tot}}) \cdot \eta_{Light \rightarrow PS_{phyto,tot}} \cdot Light, \tag{4}$$

$$\begin{aligned} I'_{zoo,tot} &= (1 - E_{I_{zoo,tot}}) \cdot \eta_{PS_{phyto,tot} \rightarrow I_{zoo,tot}} \cdot PS'_{phyto,tot} \\ &= (1 - E_{PS_{phyto,tot}}) \cdot (1 - E_{I_{zoo,tot}}) \cdot \eta_{Light \rightarrow PS_{phyto,tot}} \cdot \eta_{PS_{phyto,tot} \rightarrow I_{zoo,tot}} \cdot Light, \end{aligned}$$

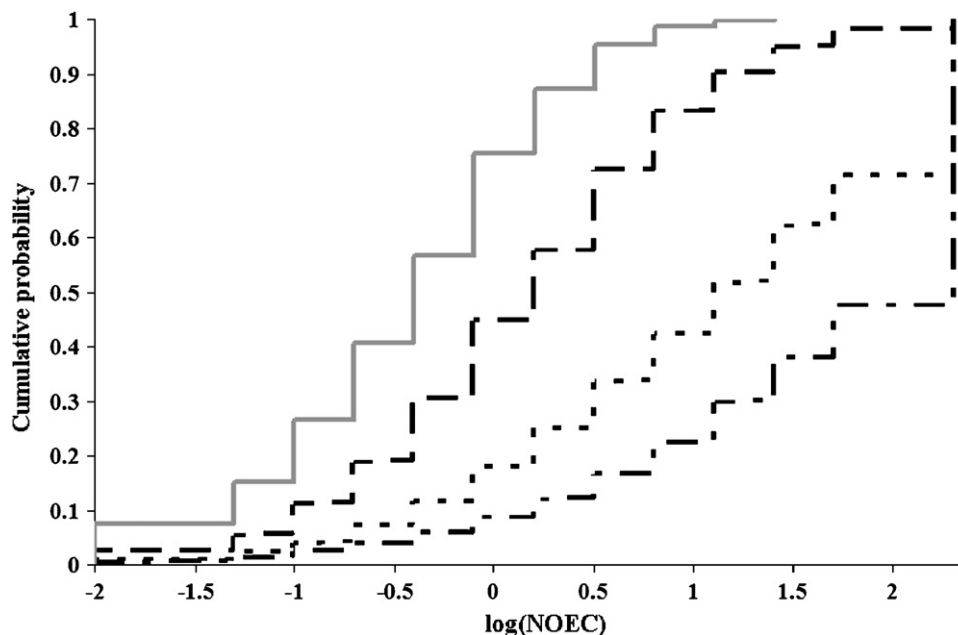


Fig. 3 – Cumulative probability distribution of grey: $\log(\text{ecosystem structure-NOECs})$; dashed: $\log(I_{\text{fish}}\text{-NOEC})$; dotted: $\log(I_{\text{zoo,tot}}\text{-NOEC})$; dotted and dashed: $\log(\text{PS}_{\text{phyto,tot}}\text{-NOEC})$.

$$I'_{\text{fish}} = (1 - E_{I_{\text{fish}}}) \cdot \eta_{I_{\text{zoo,tot}} \rightarrow I_{\text{fish}}} \cdot I'_{\text{zoo,tot}}$$

$$= (1 - E_{\text{PS}_{\text{phyto,tot}}}) \cdot (1 - E_{I_{\text{zoo,tot}}}) \cdot (1 - E_{I_{\text{fish}}})$$

$$\cdot \eta_{\text{Light} \rightarrow \text{PS}_{\text{phyto,tot}}} \cdot \eta_{\text{PS}_{\text{phyto,tot}} \rightarrow I_{\text{zoo,tot}}} \cdot \eta_{I_{\text{zoo,tot}} \rightarrow I_{\text{fish}}} \cdot \text{Light},$$

with E representing the direct effect of a toxicant on the ecosystem function indicated in subscript, and affected ecosystem functions indicated by a quotation mark ($'$). It can be readily calculated that exposing the considered ecosystem to a toxicant not directly affecting I_{fish} (i.e., $E_{I_{\text{fish}}} \approx 0$) may still result in an observable effect on I_{fish} . Assume that when exposing the ecosystem to a concentration c of this toxicant, $E_{\text{PS}_{\text{phyto,tot}}}$ and $E_{I_{\text{zoo,tot}}}$ are both 0.2, and that $E_{I_{\text{fish}}} \approx 0$. Consequently, $(1 - E_{\text{PS}_{\text{phyto,tot}}}) \cdot (1 - E_{I_{\text{zoo,tot}}}) \cdot (1 - E_{I_{\text{fish}}})$ will be 0.64, indicating a 36% effect on I_{fish} , even though I_{fish} was not directly affected (i.e., $E_{I_{\text{fish}}} \approx 0$).

As such, the trend of the relationship between NOEC and trophic level was found to be opposite for ecosystem structure ($\text{NOEC}(\text{fish}) > \text{NOEC}(\text{zooplankton}) > \text{NOEC}(\text{phytoplankton})$) and ecosystem function ($\text{NOEC}(\text{PS}_{\text{phyto,tot}}) > \text{NOEC}(I_{\text{zoo,tot}}) > \text{NOEC}(I_{\text{fish}})$). Since these trends are independent of toxicant type, explanations for these trends were sought in the ecological interactions within the system studied (see current and previous section). This confirms the importance of ecological interactions for the resulting ecological effects of toxicants. Apparently, these ecological interactions have resulted in the ecosystem structure to be almost consistently as or more sensitive than the ecosystem function in the ecosystem studied. Whether this will be the case in other systems will depend on the food web's configuration and its constituents. In particular, the results obtained here should not be extrapolated to ecosystems with a higher diversity than the system studied here. The possible presence of one or more keystone species (Mills et al., 1993; Menge et al., 1994)

will likely make certain ecosystem functions more sensitive than suggested here. However, whether a higher diversity necessarily results in the presence of keystone species, i.e., in less functional redundancy, is still under debate in ecological literature (Hooper et al., 2005). Once a better insight is gained into these issues, more complex experiments can be designed to elucidate the relation between the sensitivity of ecosystem structure and function in ecosystems with a higher diversity.

4. Conclusions

For 979 of 1000 hypothetical toxicants, the ecosystem structure-NOEC was lower than or equal to the ecosystem function-NOEC, indicating that the ecosystem structure is as or more sensitive than the ecosystem function for those toxicants. Hence, the tested assumption T3 was found to be valid for the tested ecosystem. For 239 of these 979 toxicants, both NOECs were equal. For half of the 1000 toxicants, the structure of lower trophic levels (i.e., phytoplankton) appears to be more sensitive than the structure of higher trophic levels (i.e., fish). As such, ecosystem structure-NOECs are primarily determined by the sensitivity of the structure of lower trophic levels. In contrast, ecosystem functions associated with higher trophic levels (e.g., total ingestion by fish) are more sensitive than functions associated with lower trophic levels (e.g., total photosynthesis by phytoplankton) for 749 toxicants. Top-down regulation of the ecosystem structure and cascading effects on lower trophic level functions to higher trophic level ecosystem functions are discussed as possible explanations for these two contrasting findings.

Appendix A. Supporting Information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.watres.2008.01.006.

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