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June 2002

Jul 1st, 12:00 AM

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Indirect Effects in Ecosystems: a Review of Recent Modelling Studies and a Methodological Framework for Comparative Theoretical Analysis

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Abstract: Indirect interrelations between ecosystem processes are often realised after a considerable time lag, and, therefore, are easily overlooked. The understanding of these relationships, however, is indispensable for sustainable development and ecomanagement. Investigation of mechanisms underpinning complex indirect delayed relationships is greatly aided by advanced mathematical techniques, including correlation, multiple regression and factor analysis, simulation modelling, etc. This paper provides a brief review of the recent relevant studies. These techniques may be especially useful if used in concert on a range of ecosystems, thus integrating the information obtained in a comparative theoretical ecosystem analysis (CTEA). A methodological framework for CTEA is given and possible implications discussed.

Keywords: indirect interactions, ecosystem processes, integrative approach

1. PREAMBLE

Some of the interrelations between ecosystem processes are fairly straightforward and, therefore, obvious. Others, however, are indirect and often realised only after a considerable time lag. For example, the dramatic increase in volcanic activity (possibly caused by the impact of an asteroid) at the end of the Mesozoic era is thought to have led to the extinction of dinosaurs, which arguably stimulated the eventual evolution of mammals (including humans). The increased production and use of fertilisers in the 1950s led to the increased phosphate inputs, eutrophication and decrease in water quality in many lakes, ponds and reservoirs during the subsequent decades. The increased consumption of fossil fuels in the 20th century led to the increased emissions of carbon dioxide, which were eventually followed by global warming and an apparent increase in the frequency of natural disasters. This climate change was probably accelerated by the depletion of the planet's ozone layer due to the CFC (chlorofluorocarbon) containing deodorants and refrigerants.

Hence, there are examples of indirect delayed relationships in natural systems, including the global one – the Biosphere. The majority of these relationships remain either overlooked or poorly understood. Their modelling analysis is not straightforward, and often requires a high level of submodel integration due to the complexity of processes involved. This analysis, however, may be facilitated by a targeted use of mathematical techniques. The present paper gives a brief review of recent relevant studies, and a framework summary of the approaches and methods used.

2. DEFINITIONS

There have been many definitions of direct and indirect effects [see references in Fath & Patten, 1999]. Usually, the interactions between two components not involving direct transfer of energy and/or matter are viewed as indirect, while those which involve an explicit direct transaction are viewed as direct [see, e.g. Fath & Patten, 1998, 1999; and references therein]. A more precise classification accounts for the distinction between those effects that are directly and indirectly mediated [*sensu* Krivtsov, 2001], since the latter ones are particularly difficult to observe, especially if the cause and effect are substantially separated in time [Krivtsov et al., 2000]. For the purpose of this paper, both directly and indirectly mediated effects will be treated as indirect, but the distinction will be made where deemed appropriate.

3. RECENT STUDIES OF INDIRECT RELATIONSHIPS

The information about recent modelling research involving analysis of indirect relationships in ecological systems was obtained via an SCI search using the following keywords combination: 'ecological interactions' and 'indirect' and 'model' or 'ecosystem' and 'indirect' and 'model'. The search returned 70 articles, but more than half of them were judged as irrelevant (e.g. a very common case was related to those studies were either indirect estimates or indirect measurements were carried out, but not modelling of indirect relationships; another typical case comprised the studies were modelling was only suggested). The majority of

the remaining papers came from Ecological Modelling, while the main topics appeared to be concerned with issues of climate change (mainly in relation to terrestrial environment), and aquatic ecosystem dynamics. A brief overview given below contains some examples from the references found, together with some others, not returned by the search.

3.1 Aquatic Studies

Carrer and Opitz [1999] investigated indirect interactions in the Lagoon of Venice using 'Ecopath', a software implementing methods of network analysis. Among other interesting relationships, they found that about half of the food of nectonic benthic feeders and nectonic necton feeders passed through detritus at least once, whilst there was no direct transfer of such food according to the diet matrix. The paper contains a number of references to other studies where Network analysis was used to analyse indirect relationships among ecosystem components [see also Patten, 1992; Fath and Patten, 1998, 1999, and references therein].

Modifications of the model CASM were used by Bartell et al. [1999] and Naito et al. [2002] to study direct and indirect effects in the aquatic ecosystems of Canada (Quebec) and Japan (lake Suwa) respectively. Numerical sensitivity analysis was applied in both cases (sensitivity of a state variable on changes in a parameter was measured as the percent change from the reference situation). For the Canadian case study it was found that variability in the production of macrophyte population determines an indirect risk component of toxic Hg effects on phyto- and zooplankton, periphyton and fish. In the Japanese case study it was found that the annual production of piscivorous fish was considerably influenced by the optimal consumption temperature of certain benthic insects. Another interesting finding was that the physiological parameters of the diatom *Melosira* were the important sources of the cyanobacterium *Microcystis* production variability. Although the authors did not make a detailed interpretation of the latter relationship, their results suggest that the underlying mechanism might be a common inverse relationship between spring diatom and summer cyanobacterial blooms (see references related to the Rostherne Mere case study below).

Hanratty & Liber [1996] studied indirect effects of a pollutant diflubenzuron on growth of larval bluegill sunfish in a littoral enclosure. At very high concentrations the model predictions were good, but at intermediate concentrations the accuracy was variable, with some indirect responses being exaggerated due to cascading effects through the ecosystem trophic levels.

McClanahan and Sala [1997] used a simulation model of the Mediterranean infralittoral rocky bottom to study possible effects of various management options. Running a number of 'What if' scenarios they concluded that many of potential changes are likely to be indirect effects caused by changes in trophic composition. For example, if invertivorous fish were removed as part of a management scenario, sea urchins would reduce algal abundance and primary production, leading to competitive exclusion of herbivorous fish. Although similar interactions were known from tropical seas, these results were not anticipated by previous field studies in the Mediterranean.

Loladze et al. [2000] investigated how the interactions between phytoplankton and zooplankton change if the Lotka-Volterra model incorporates chemical heterogeneity for both trophic levels. It was found that indirect competition between two populations for P can shift the relationship from a usual (+,-) type to an unusual (-,-) type, leading to a very complex overall dynamics.

Hulot et al. [2000] compared the performance of linear food chain models and an intermediate complexity model, applied to data of a mesocosm experiment simulating lake nutrient enrichment. The intermediate complexity model (with separation of trophic levels into functional groups according to size and diet) was the only one which performed satisfactory, thus highlighting the importance of functional diversity and indirect interactions.

Malaeb et al. [2000] used structural equation modelling (a technique combining path, factor, and regression analyses) to estimate the contribution of indirect effects of sediment contamination and natural variability on biodiversity and growth potential in a selection of North American estuaries. They found that a positive indirect effect of natural variability (mediated through biodiversity) on growth potential exceeded a direct negative effect, resulting in the overall positive relationship.

Detailed attention to indirect effects was given in a number of studies conducted at Rostherne Mere, one of the best studied lakes in UK [see Krivtsov et al., 1998, 1999, 2001, and references therein]. Indirect effects were shown to occur on (and across) various levels of organisation, including intracellular, population and ecosystem levels. Statistical analysis of the observed datasets and sensitivity analysis (using mathematical model 'Rostherne') were used to elicit the hidden relationships between Si and P biogeochemical cycles coupled through the dynamics of primary producers [Krivtsov, 2001; Krivtsov et al., 2000]. It was shown that there is an inverse relationship between spring diatom

and summer cyanobacterial blooms, which could be utilised as a new method of eutrophication control. Dynamic ecosystem modelling revealed a complex interplay between direct and indirect effects in the ecosystem, including those related to the influences of temperature, light, inflow/outflow characteristics, and interactions among nutrients, algae, detritus, zooplankton and fish. These analyses have led to the derivation of the 'Indirect regulation rule for consecutive stages of ecological succession', which generalised the most notable interdependencies observed for other types of ecosystems [Krivtsov et al., 2000], and to a general classification of the ecosystem effects referred to in definitions [Krivtsov, 2001].

Indirect interrelations between Si and P availability were also addressed by Dippner et al. [1998]. On the basis of a simple numerical model it was concluded that indirect effect of the silicate reduction in coastal waters causes an increased flagellate bloom, due to a high availability of riverborne nutrient loads. These conclusions are highly in line with the results related to lakes Suwa and Rostherne Mere quoted earlier.

3.2 Climate Change Studies

A number of studies related to investigation of global climate change. Norberg & DeAngelis [1997] used a model of a closed phytoplankton-zooplankton ecosystem to investigate effects of temperature, light and nutrients, while the majority of studies concentrated on the responses in the terrestrial environment. Riedo et al. [1999] forced a dynamic ecosystem model with weather scenarios derived using a general circulation model. The simulated increase of shoot dry matter was attributed to the combination of direct effects of CO_2 and increased T, and indirect stimulation via increased N availability. The results also highlighted the importance of site-specific analysis.

McMurtrie & Comins [1996] used the forest ecosystem model G'DAY to investigate possible responses to the elevated CO_2 concentration. The analysis showed that responses on different timescales are determined by different ecosystem-level feedbacks, thus the magnitude and even growth response to an increase in atmospheric CO_2 may be variable.

In another study vanMinnen et al. [1995] used the terrestrial carbon cycle submodel of the IMAGE 2 model to analyse the importance of feedback processes on global and regional scale. Simulations were carried out using all combinations of CO_2 fertilisation, temperature effect on plant growth, and climate impact on

soil decomposition. Consequently, strong nonlinearities between contributions of separate and combined feedback factors were reported.

Vukicevic et al. [2001] developed a number of versions of a simplified spatially aggregated model, consisting of the following compartments: atmospheric CO_2, vegetation, and 2 soil pools with different turnover times. One of the versions also included N cycle. The results indicated that the effects of temperature on ecosystems are manifested as a combination of direct physiological and indirect lagged responses, and the combined effect may therefore depend upon specific conditions. For instance, warming and longer growing seasons in high latitudes could either increase or decrease NEP, depending whether indirect feedbacks of nutrients are larger or smaller than the direct effects on NPP and respiration.

van Oene et al. [1999] modelled increased CO_2 and N deposition effects on a natural vegetation succession on Dutch inland dunes. It was concluded that indirect effects through changing competitive relations between species might be more important then direct effects.

Dale et al. [1991] used a population model in the site-specific ecological context to predict effects of infestation of fir trees by the balsam woolly adelgid (BWA). The model suggested that temperature may have an indirect influence on a spatial pattern of living trees through effects on BWA survival and development.

Rathgeber et al.[2000] used a biogeochemistry model BIOME3 to study direct and indirect effects of elevated CO_2 on pine(*Pinus cembra*) productivity. It was concluded that in this case direct effects will be prevalent. Post & Pastor [1996] showed, using an individual-based forest ecosystem model LINKAGES, that climate change results in a complex combination of direct and indirect responses, and that the exact outcome depends on the peculiarities of any particular scenario. Modelling aspects and relative importance of direct and indirect effects of climate change on forests was also addressed in the review by Loehle & LeBlanc [1996].

3.3 Other studies

Fath & Patten [1998] used methods of network analysis to show that, in the ecosystem context, direct transactions between organisms produce integral effects more positive than a simple sum of direct effects [see also Patten, 1992]. This was in line with the view that mutualism is an implicit consequence of indirect interactions and ecosystem organisation, and that the contribution of positive relationships should increase along the course of evolution and ecological succession.

Sinclair et al. [2000] analysed results of a comprehensive experiment conducted in a Canadian boreal forest, where 7 different perturbations either removed or supplemented original trophic levels. Subsequent changes in biomass of the other levels were compared with the predictions of 27 simple models testing linear interactions. The authors concluded that observed indirect effects were weak, and rapidly attenuated along the food chain. It should be noted, however, that, in fact, the study analysed only directly mediated effects [*sensu* Krivtsov, 2001], and did not attempt to account for indirectly mediated ones.

Leriche et al. [2001] applied the PEPSEE-grass model to a West African humid grassland. They found that the response of NPP to grazing intensity was a complex result of both direct and indirect effects of biomass removal on soil water availability, grass nitrogen status and productivity, light absorption efficiency, and root/shoot allocation pattern.

Intachat et al. [2001] used stepwise regression analysis to model the effect of weather variables on the phenology of Malaysian rain forest and the abundance of geometroid moths. Due to coupled delayed meteorological effects, the abundance of certain moth species appeared to precede trees flushing, flowering and fruiting, which must be beneficial for emerging larvae.

Bockstael et al. [1995] published a progress report on their ongoing attempt to integrate the Patuxent Landscape Model (PLM) with a number of economic submodels. The authors give a brief mentioning of previous 'attempts to grapple with interactions of ecological functions and economic actions', and imply that their study will be the first one to provide a really good insight into indirect ecosystem effects of current policy options over long time horizons. There appears to have been substantial progress since then: 29 articles refer to this paper, and the readers may wish to follow up the developments on the matter.

Among other studies it is worth mentioning the papers of Daufresne & Loreau [2001], who examined the interactions between primary producers and decomposers in a simple ecosystem using a stoichiometrically explicit model, and Loreau [1998], who showed that certain changes in ecosystem properties are indirect results of selection for different traits in organisms,

3.4 Limitations and implications

It should be noted that the selection of cited papers was limited by the keywords used, limitations of the database (e.g. bias to English language journals, restriction of the scope to titles, abstracts and keywords, etc.). Hence,

quite a few relevant papers were not found by the search. It is also worth pointing out that the earliest reference found by the search was published in 1991, although the database goes back to 1981. This, of course, does not mean that the work on modelling indirect interactions had not been carried out prior to that (indeed, many papers referred to earlier work). However, it has clearly indicated that the investigations of indirect interrelations in ecological systems using mathematical modelling has greatly intensified during the last decade. I suggest that such investigations are now becoming sufficiently widespread to warrant development of a methodological framework for theoretical analysis of the patterns observed.

4. COMPARATIVE THEORETICAL ECOSYSTEM ANALYSIS

The approaches used in the studies reviewed above can be summarised in a methodological framework for analysis of indirect relationships in ecosystems. This will allow the scientific community to better understand and classify such relationships, and will greatly facilitate further investigations, particularly related to the assessment of subtle differences in the indirect effects due to peculiarities of particular ecosystems.

Within the proposed framework, the CTEA may comprise 3 stages outlined below. An important prerequisite for CTEA is availability of data from detailed monitoring studies. At stage 1, the data from each ecosystem are analysed independently using a suit of statistical techniques and methods of network analysis, and the interrelations observed are then incorporated in the process-based simulation models, constructed, e.g., using differential equations or agent-based modelling. At stage 2, a complete sensitivity analysis of the simulated dynamics of output variables on input values is carried out for each model. The indirect relationships revealed by sensitivity analysis are then interpreted in terms of the existing ecological knowledge. If a variable is found to be sensitive to changes in apparently unrelated input, then either model definitions or the existing ecological theories are likely to require amendments [see e.g. Krivtsov et al., 2000]. Statistical techniques might once again help interpretation of the peculiarities observed. At stage 3, the indirect delayed relationships found at previous stages could be classified in relation to the underlying mechanisms and peculiarities of their manifestation. The latter could then be used to assess the differences between different types of ecosystems (e.g. aquatic versus terrestrial), or differences related to small

variation in ecosystem structure (e.g. absence/presence and representation of trophic levels, composition of a guild, parameters of physical environment, etc.). The hypotheses about the discovered relationships could now be tested using structural equation modelling [see above the example of Malaeb et al., 2000, and references therein], and the whole process may need to be repeated from stage 1, particularly if additional data are available.

Although there seems to be no research that has yet rigorously followed all the sequence described above, the components of the methodological framework presented here were variously applied in studies reviewed in section 3. For example, in the Rostherne Mere case study, a comprehensive data set was analysed by means of statistical techniques, which facilitated the construction of a dynamic simulation model (stage 1). This was then followed by an extensive sensitivity analysis, which revealed a number of unexpected relationships (e.g. between winter concentration of dissolved Si and summer cyanobacterial maximum). These results were then confirmed by new statistical analysis, and ultimately resulted in changes of the contemporary theory (stage 2). Then some of the indirect relationships studied were classified in relation to the underlying mechanisms (i.e. in this case directly- and indirectly mediated), which facilitated extrapolation of the conclusions for other types of ecosystems (stage 3). A number of 'what if' scenarios examined provided information on the differences of manifestation of the indirect effect of Si on cyanobacterial bloom in relation to, e.g., hydrological and morphological parameters, thus assessing differences between ecosystem types (e.g. deep versus shallow lakes, lakes with high versus lakes with slow retention time). It is intended that further work should involve application of structural equation modelling, and the comparison with the indirect relationships revealed for a terrestrial ecosystem [see Walker et al., this issue].

The methodological framework presented here is aimed at bringing together separate lines of current investigations, hence combining them in an integrative approach. Further development and systematic application of CTEA is vital for accurate ecological forecasting, and has, therefore, potential societal benefits related to issues of environmental impact assessment and sustainable development.

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