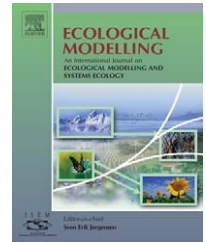


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## Effective trophic positions in ecological acyclic networks

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### ABSTRACT

In the tropho-dynamic analysis of ecosystems the heuristic, discrete concept of trophic level has been replaced by the more realistic, continuous definition of trophic position. In ecological network analysis (ENA) the suite of matrix manipulations called canonical trophic aggregation (CTA) apportions each species' feeding activity to a series of discrete trophic levels sensu Lindeman. The effective trophic position is computed as the sum of the fractions of trophic activity that each species performs at different trophic levels. In this paper we present an extension of the CTA that combines matrix manipulation and sensitivity analysis. Applying this "extended" CTA to an hypothetical network and to real ecosystems we show how trophic position can be computed taking into account the contribution of external inflows, making it scale-insensitive. Moreover "extended" CTA solves ambiguities related to trophic position in the presence of multiple non-living nodes, considering them as imports.

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## 1. Introduction

The trophic level ideal of a simple linear chain of energy passages had great appeal as an easy and intuitive description of complex energy-based ecosystem processes. Further, this approach has inspired several applications in ecology and management such as the cascade trophic interaction theory (Carpenter et al., 1986; Carpenter and Kitchell, 1993) and the associated biomanipulation idea (Gophen, 1990; Shapiro, 1990). On the other hand, the structural intricacy (e.g. richness and topology of connections between species) of food webs gives rise to a vast array of functional behaviors that do not easily accommodate into the framework of the "green world"

theories (Polis and Strong, 1996). Donor-controlled diffuse omnivory, for example, shunts the flow of matter and energy away from adjacent trophic components thus challenging the idea that populations aggregate into discrete homogeneous trophic levels each of which receives energy solely from its adjacent level nearer the ultimate source of energy (the outside or abiotic environment) and passes it to the next (Vadas, 1990; Winemiller, 1990; Polis, 1991, 1994). The "...hawk that feeds at five trophic levels ..." (Cousins, 1985, 1987) embarrasses less the ecologists now that the trophic-dynamic description of the ecosystem needs not exclude the reticulate connections between the diversity of consumers and resources. Mapping energy movements according to feeding relation in

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