

### 3.16 Linking mediation and time forcing functions to trophic interaction rates

The basic Ecosim prediction for "flow" rate of type- $i$  prey biomass to type- $j$  predators is of the functional form

$$\text{flow (biomass/time)} = a_{ij} \cdot V_{ij} \cdot P_j$$

where  $a_{ij}$  is a "rate of effective search" parameter,  $V_{ij}$  is vulnerable prey biomass, and  $P_j$  is effective predator abundance (for simple models  $P_j$  is just predator biomass; for multi-stanza groups it is the sum over ages in that group of numbers at age times body weight to the 2/3 power, an index of per-predator search rate). If vulnerable prey were randomly distributed over the modelled spatial area, and  $V$ ,  $P$  were expressed as abundances per unit area, then  $a_{ij}$  would be interpretable as a volume or area swept per unit predator abundance (per  $P_j$ ) per unit time, corrected for the proportion of time actually spent searching for food (foraging time and handling time adjustments reduce  $a_{ij}$  from its theoretical maximum value for a predator that searched all the time for food).

To understand how effects of habitat changes as represented through time forcing functions, and mediation effects as expressed through mediation functions of abundances of other organisms, are likely to affect trophic flow rates, we need to be a bit more careful about the  $a_{ij}$  parameter. In particular, we need to recognize that for most trophic interactions, predators search for prey only over restricted spatial foraging arenas, and hence  $V_{ij}$  is distributed only over such areas rather than at random over the whole system. Suppose the (practically unmeasurable) restricted area where foraging by  $j$  on prey  $i$  takes place is  $A_{ij}$  per unit total model area. Suppose that while in this area, each unit of predator abundance (per  $P_j$ ) searches an effective area  $a^*_{ij}$  for prey. On average, each such area searched should result in capture of  $V_{ij}/A_{ij}$  prey, since this ratio is prey density in the arena area. In other words, the flow rate could be modelled more precisely (if we could measure  $A_{ij}$ ) as

$$\text{flow rate} = a^*_{ij}/A_{ij} \cdot V_{ij} \cdot P_j$$

i.e., the basic Ecosim equation's  $a_{ij}$  can be interpreted as  $a_{ij} = a^*_{ij}/A_{ij}$ . Expressed this way, we see that time forcing and/or mediation effects can influence the flow rate in at least three quite distinct ways:

- by altering the effective search rate  $a^*_{ij}$  of the predator, for example by using a turbidity time forcing function or a mediation function of algal biomass that reduces  $a^*_{ij}$  at high algal biomass;
- by altering the area  $A_{ij}$  over which vulnerable prey and/or predators are distributed, for example by a mediation effect where macrophyte or seagrass biomass limits the foraging area usable by small predatory fish, so increases in those plant biomasses should be represented as causing increases in  $A_{ij}$  for all prey  $i$  of the small fish as predator  $j$ . Another example would be restriction of  $A_{ij}$  for feeding on small fishes by pelagic birds caused by large pelagic fishes, which drive small fishes nearer to the surface where they are more available to the birds.
- by altering the [vulnerability exchange rates](#)  $v_{ij}$  that determine (along with  $a^*_{ij}/A_{ij}$ )  $V_{ij}$  from total prey biomass  $B_i$  (the basic equation for  $V$  from  $B$  is  $V_{ij} = v_{ij} \cdot B_i / (v_{ij} + v'_{ij} + a^*_{ij}/A_{ij} P_j)$ ). For example, if small fish respond to increased large plant biomass by occupying a larger area, the mixing rate ( $v_{ij}$ ) of planktonic food organisms into that larger area will increase as well.

Until recently, Ecosim only allowed users to apply a single time forcing function to each trophic flow rate (each  $i,j$ ), and only as a multiplier (with base value 1.0) on the rate of effective search  $a_{ij}$  (Case 1 above). Likewise, users could only apply a single mediation function to each flow rate, as a multiplier on  $v_{ij}$  (Case 3 above). So, for example, users could model how increases in large plant biomass affect exchange rates of food organisms into areas adjacent to where small fish hide, but not how increases in  $A_{ij}$  imply less severe intraspecific competition (reduced effect of  $P_j$  on  $V_{ij}$ ) and also reduced predation rates on  $j$  when it is spread over a larger area relative to its predators. Further, they could not represent such multiple impacts as reduced foraging efficiency (lower  $a^*_{ij}$ ) associated with increased algal abundance, or reduction in area occupied by macrophytes due to shading by the algae.

We now allow users to apply up to 5 different multiplier (time forcing and/or mediation) functions to each trophic flow ( $i,j$ ) rate prediction, and to specify whether each function multiplies  $a^*_{ij}$ ,  $A_{ij}$  and/or  $v_{ij}$ . Two simple forms are used to specify these multiplier options, and it is invoked simply by clicking on the  $i,j$  cell in the Ecosim [Apply forcing function \(consumer\)](#) or [Apply mediation](#) forms. Using these forms, users can choose the parameter which is multiplied by each forcing or mediation function, i.e. one of the following choices:

- Multiply overall predator rate of effective search ( $a_{ij}$ ), for example to represent time-varying turbidity changes that affect predator search efficiency or mediation effects of algal biomass on search efficiency.
- Multiply vulnerability exchange rate ( $v_{ij}$ ), for example to represent increased movement rates of prey into vulnerable behavioural state at times when water mixing rates are higher;
- Multiply area of foraging arenas (divide  $A_{ij}$  by multiplier), for example to represent increase in habitat area available for juvenile fish refuges;
- Multiply area (divide  $A_{ij}$ ) and also multiply  $v_{ij}$  for example to represent increase in safe foraging habitat available to a predator that feeds on prey that become available in foraging arenas through passive drift/mixing processes such that increasing area used by predator results in higher proportion of total prey population being available in foraging areas at any moment.

Forms for setting up forcing and trophic mediation functions in Ecosim are found under the Ecosim input section of the *Navigator window* ( *Time Dynamic (Ecosim)* > *Input* > *Forcing function*; and *Time Dynamic (Ecosim)* > *Input* > *Mediation*; see [Forcing function](#) and [Mediation](#)).