$$Q = \begin{vmatrix} -\sum_{s \neq B} q_{Bs} & q_{BM} & q_{BP} & 0 \\ q_{MB} & -\sum_{s \neq M} q_{Ms} & q_{MP} & q_{MT} \\ q_{PB} & q_{PM} & -\sum_{s \neq P} q_{Ps} & q_{PT} \\ 0 & q_{TM} & q_{TP} & -\sum_{s \neq T} q_{Ts} \end{vmatrix}$$

$q_{rs} = q_{rs.0} \times \exp(\beta_{rs.1} \times climate + \beta_{rs.2} \times soil + \beta_{rs.3} \times disturbances)$

for $r \neq s$ and $s \neq$ Pioneer

$q_{rs} = q_{rs.0} \times \exp(\beta_{rs.3} \times disturbances)$

for $s =$ Pioneer