



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

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

for  $r \neq s$  and  $s \neq \text{Pioneer}$

$$q_{rs} = q_{rs,0} \times \exp(\beta_{rs,2} \times \text{disturbances})$$

for  $s = \text{Pioneer}$