influence on species \( i \). An alternate, visual representation captures the same ideas in a directed graph (also called digraph) in which nodes represent species and arrows between them represent the mutual interactions, as shown in Figures 6.10 and 6.11. The question is then whether it can be concluded, from this graph or sign pattern only, that the system is stable. If so, the system is called qualitatively stable.

(a)

(b)

(c) Signed directed graphs (digraphs) can represent species interactions in an ecosystem. The graphs shown here are equivalent to the matrix representation of sign patterns given in the text (a) example 2, (b) example 3, and (c) example 4.
Example 2
Here we study the sign pattern of the community described in equations (21a, b, c) of Section 6.4. From Jacobian (24) of the system we obtain the qualitative matrix

\[ Q = \text{sign } J = \begin{bmatrix} 0 & + & + \\ - & 0 & 0 \\ - & 0 & - \end{bmatrix}. \]

This means that close to equilibrium, the community can also be represented by the graph in Figure 6.10. Reading entries in \( Q \) from left to right, top to bottom:

Species 1 gets positive feedback from species 2 and 3.
Species 2 gets negative feedback from species 1.
Species 3 gets negative feedback from species 1 and from itself.

Example 3 (Levins, 1977)

In a closed community, three predators or parasitoides, labeled \( P_1, P_2, \) and \( P_3, \) attack three different stages in the life cycle of a host, \( H_1, H_2, \) and \( H_3. \) The presence of hosts is a positive influence for their predators but predators have a negative influence on their prey. Figure 6.10(b) and the following matrix summarize the interactions:

\[
\begin{array}{cccccc}
& P_1 & P_2 & P_3 & H_1 & H_2 & H_3 \\
\hline
P_1 & 0 & 0 & 0 & + & 0 & 0 \\
P_2 & 0 & 0 & 0 & 0 & + & 0 \\
P_3 & 0 & 0 & 0 & 0 & + & \\
H_1 & - & 0 & 0 & - & 0 & + \\
H_2 & 0 & - & 0 & + & - & 0 \\
H_3 & 0 & 0 & - & 0 & + & - \\
\end{array}
\]

Note that \( H_1, H_2, \) and \( H_3 \) each exert negative feedback on themselves.

Example 4 (Jeffries, 1974)

In a five-species ecosystem, species 2 preys on species 1, species 3 on species 2, and so on in a food chain up to species 5. Species 3 is also self-regulating. A qualitative matrix for this community is

\[
Q = \begin{bmatrix} 0 & - & 0 & 0 & 0 \\ + & 0 & - & 0 & 0 \\ 0 & + & - & - & 0 \\ 0 & 0 & + & 0 & - \\ 0 & 0 & 0 & + & 0 \end{bmatrix}
\]

See Figure 6.10(c).
qualitative stability. Suppose \( a_{ij} \) is the \( ij \)th element of the matrix of signs \( Q \). Then it
is necessary for all of the following conditions to hold:

1. \( a_{ii} \leq 0 \) for all \( i \).
2. \( a_{ij} < 0 \) for at least one \( i \).
3. \( a_{ij}a_{ji} \leq 0 \) for all \( i \neq j \).
4. \( a_{ij}a_{jk} \cdots a_{qr}a_{rl} = 0 \) for any sequences of three or more distinct indices \( i, j, k, \ldots, q, r \).
5. \( \det Q \neq 0 \).

These conditions can be interpreted in the following way:

1. No species exerts positive feedback on itself.
2. At least one species is self-regulating.
3. The members of any given pair of interacting species must have opposite effects on each other.
4. There are no closed chains of interactions among three or more species.
5. There is no species that is unaffected by interactions with itself or with other species.

For mathematical proof of these five necessary conditions, consult Quirk and Ruppert (1965). May (1973) and Pielou (1969) comment on the biological significance, particularly of conditions 3 and 4. The conditions can be tested by looking at graphs representing the communities. One must check that these graphs have all the following properties:

1. No + loops on any single species (that is, no positive feedback).
2. At least one – loop on some species in the graph.
3. No pair of like arrows connecting a pair of species.
4. No cycles connecting three or more species.
5. No node devoid of input arrows.

These five conditions are equivalent to the original algebraic statement.

---

**Example 5**

For examples 2 to 4 we check off the five conditions given earlier:

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<th>Example 3</th>
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