State-dependency of process rates: a clear concept of feedback in ecology

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The complexity of biological systems motivates a search for invariant patterns (signatures) that indicate which kinds of dynamics a system can exhibit, without requiring a complete mathematical description and analysis of the system. An important class of signatures deals with feedback loops, i.e. closed chains of interaction among state variables in a dynamical system [1-9]. However, while the concept of feedback has proved useful in regulatory biology [3,10-12], ecological science usually deals with feedback in a most armwaving manner [13,14].

Four incompatible definitions of feedback currently coexist [1-4]. Opinions differ on whether the sign of links in a feedback loop is determined by the direction of processes themselves1, or how process rates respond to changes in system state. In the latter case, a self-effect (a state variable's direct effect on itself) may appear qualitatively different depending on whether one considers the state-dependency of the relative [2] or the absolute3 rate-of-change of the variable. A fourth definition uses "feedback" as a summary measure of all disjunct loops of action in the system [4].

Without an unambiguous operational definition of positive and negative feedback, ecological and biological science is ill-equipped to meet current challenges in making sense of complex systems. Gene regulatory research produces huge amounts of data on the complex interplay of positive and negative feedback, calling for algorithms for automated detection of feedback loops. Similar challenges apply in community ecology [2] and social dynamics.

We evaluate the four candidate feedback definitions for mathematical and conceptual consistency. We favor definition [3] for its proven track record [6,15-18], its reference-frame independence, and its link to classical stability analysis [19]. Because the state-dependency of process rates is such a fundamental feature of natural dynamical systems, this feedback concept offers heuristic promise for

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conceptual explanation and hypothesis generation, also beyond the framework of ordinary differential equations.

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