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AN INDEX THEOREM FOR DISSIPATIVE SEMIFLOWS

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Dedicated to the memory of Geoffrey J. Butler

1. Introduction. Deterministic modelling in the biological sciences often leads to ordinary differential equations defined on the state space $\mathbf{R}_+^n$, each coordinate representing the population density of a component or "species" of the system. If only the relative population frequencies are of interest, or some conservation of total mass holds, then the state space reduces to the probability simplex $S_n = \{\mathbf{x} \in \mathbf{R}_+^n : \sum x_i = 1\}$. Often the boundary and hence the interior of the state space $\mathbf{R}_+^n$ or S_n is invariant under the flow as in ecological models, meaning that a species absent at time 0 will not appear at any future time. This leads to *ecological differential equations*

$$\dot{x}_i = x_i f_i(\mathbf{x}). \tag{1}$$

This is not true, however, for more general models, as in population genetics (selection models including mutation, recombination, or differential fertilities), epidemiology, ecological models with migration, or chemical reaction kinetics. Here $\mathbf{R}_+^n$ (as well as its interior) is only forward invariant, i.e., if $x_i(0) \geq 0$ (respectively > 0) for all i, then $x_i(t) \geq 0$ (respectively > 0) for all $t \geq 0$. Then $\operatorname{bd} \mathbf{R}_+^n$ is not invariant but "semipermeable." If the state space is strictly forward invariant (the flow being transverse to the boundary) then *Brouwer's degree theory* implies that the sum of the indices over all (interior) fixed points equals $+1$. Quite often, however, part of the boundary is invariant. Then some of the boundary fixed points have to be included in this index theorem.

We first single out these special boundary fixed points, which we call *saturated fixed points*. In §2 we describe some elementary properties and state the index theorem under the assumption that all of them are regular. The proofs are given in §3. In §4 a generalization to isolated fixed points is indicated, using the concept of the *boundary index*. This also allows an extension of the *Poincaré-Hopf theorem* to semiflows on