Chapter 8
Inferences About Coupling from Ecological Surveillance Monitoring: Approaches Based on Nonlinear Dynamics and Information Theory

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> *"It is far better to foresee even without certainty than not to foresee at all."*
>
> *- H. Poincare*

> *"Physics envy is the curse of biology"*
>
> *- J. Cohen*

Abstract Some monitoring programs for ecological resources are developed as components of larger science or management programs and are thus guided by a priori hypotheses. More commonly, ecological monitoring programs are initiated for the purpose of surveillance with no a priori hypotheses in mind. No conceptual framework currently exists to guide the development of surveillance monitoring programs, resulting in substantial debate about program design. We view surveillance monitoring programs as providing information about system dynamics and focus on methods for extracting such information from time series of monitoring data. We briefly describe methods from the general field of nonlinear dynamics that we believe may be useful in extracting information about system dynamics. In looking at the system as a network of locations or components, we emphasize methods for assessing coupling between system components for use in understanding system dynamics and interactions and in detecting changes in system dynamics. More specifically, these methods hold promise for such ecological problems as identifying indicator species, developing informative spatial monitoring designs, detecting ecosystem change and damage, and investigating such topics as population synchrony, species interactions, and environmental drivers. We believe that these ideas and methods provide a useful conceptual framework for surveillance monitoring and can be used with model systems to draw inferences about the design of surveillance monitoring programs. In addition, some of the current methods should be useful with some actual ecological monitoring data, and methodological

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extensions and modifications should increase the applicability of these approaches
to additional sources of actual ecological data.

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1 Introduction

The monitoring of ecological systems is an activity that is increasingly common
throughout the world [YNB01] and, as such, is beginning to be accompanied by
increased scrutiny, as scientists and natural resource managers seek to insure that
scarce funds are expended wisely. Scrutiny has been focused on topics ranging
from the reasons for monitoring, to the selection of system attributes to be
monitored, to the manner in which selected system attributes are estimated. Indeed,
Yoccoz et al. [YNB01] challenged those engaged in the conduct or development
of monitoring programs to pose the three basic questions: why, what, and how?
They emphasized that answers to the what and how questions are conditional on the
answer to the question, why monitor?

We begin by asserting that monitoring is not a stand-alone activity but is
most usefully viewed as a component of a larger program of either science or
management [Njd00, YNB01, NW06]. The role of monitoring in most scientific
programs is to provide data on changes in system variables that can be used
to confront predictions from models of competing hypotheses about system dy-
namics [HM97, WNC02, NW06]. This confrontation can lead to a rejection of
hypotheses under some approaches to science and to a change in the likelihoods
or degrees of faith associated with the different hypotheses under other approaches
to science. The roles of monitoring in most management programs similarly include
confrontation with predictions from models of competing hypotheses about system
responses to management, as well as provision of estimates of system state for use
in making state-dependent decisions, and estimates of state and related variables for
use in judging management effectiveness.

We view these uses of monitoring in the conduct of science and management as
ideal, in the sense that monitoring results play a key role in discriminating among
competing hypotheses and in making informed management decisions. However,
we believe that many monitoring programs have not been developed to discriminate
among a priori hypotheses about system behavior or to provide estimates of system
state for the purpose of making state-dependent management decisions. We will
refer to such monitoring that is not designed with reference to guiding hypotheses
about system behavior or response to management as surveillance monitoring.
We do not view surveillance monitoring as an efficient way to use conservation
funds, yet a substantial number of such programs exist worldwide. Here we consider
approaches to the analysis of such monitoring data that might be useful for trying to
learn about a system and its dynamics.

We contend that, in contrast to hypothesis-driven monitoring, no methodological framework has been presented to guide the design and analysis of surveillance monitoring data. We have noted that hypothesis-driven monitoring is used to conduct either science or management. In the case of science, there is a well-developed body of statistical theory about how to test hypotheses using collected data, both in general [Fis47, Fis58] and specifically in the case of ecological data [Hur84, SR92, SG93, WNC02]. In the case of management, a similarly well-developed body of decision theory is available to guide use of data to make optimal decisions in the face of uncertainty [Wil82, Wil89, Wil96, WNC02].

In contrast, there is a noted absence of true theory guiding the collection and use of data in ecological surveillance monitoring programs. However, investigators in other disciplines have developed theory that is relevant to investigative uses of such data, formally addressing such questions as: Are the measured data sufficient for us to understand the evolution of the dynamical system? In particular, do the measured data contain enough information to reconstruct dynamical objects of interest and recover coordinate independent dynamical properties? [OY03]. Our contention is that this work in other fields can potentially be useful in developing a general theory guiding both the collection of time series of ecological data and the use of such data in a manner that extracts maximal information about the underlying systems of interest. Although many of the methods used in the fields of physics and nonlinear dynamics were developed for long time series of relatively noise-free data, we believe that these methods have significant potential to:

1. Provide a framework for extracting information from ecological time series
2. Provide us with upper limits on the information extraction that is possible
3. Be used with data from model systems, perhaps leading to generalizations that may be useful, for example, in the design of monitoring programs
4. Be adapted or extended to deal with the sorts of short, noisy data that tend to characterize ecological time series [Bou96, Bou01, PSWM00]

We consider surveillance monitoring programs that provide time series of one or more state variables of a system of interest. State variables might be abundances of different species (e.g., a network of interconnected species), or perhaps multiple observations of the same species from a network of different spatial locations within the system. The task at hand is then to consider the time series as sources of information about the system of which they are a part and consider the kinds of information that can be extracted as well as the methods needed to accomplish this extraction. We focus on methods developed for nonlinear systems, because of the apparent prevalence of nonlinearity in ecological systems and processes [CCDD95, CDCD97, CCDDH03, DDCC95, DDCC97, HHETG93, Sch81, SEK86, Tur03]. In particular, we focus on methods for assessing coupling (dynamical interdependence; [PCH97, SSCBS96]) of different potential system components or state variables, for purposes such as:

1. Identifying whether two variables are indeed components of the same system
2. Investigating the nature of interactions among system components

3. Drawing inferences about one or more system components by monitoring
   another component(s)
4. Investigating coupling within a network of spatial locations or interrelated
   species

The methodological approaches to the investigation of coupling for nonlinear
systems have been categorized as based on either a *geometric portrait* of the
system dynamics or on the *information content* of dynamical system components.
As Sauer [Sau04] noted about the geometric approach, "The capability of these
methods for nonlinear systems, built on advanced reconstruction techniques, far
exceeds the reach of conventional signal processing." Our objective is simply to
consider the use of these approaches to extract information about systems and
their behaviors from time-series data that are collected in the absence of a priori
hypotheses and corresponding models.

We note that although we are applying the following techniques to the specific
settings of ecological monitoring of a network of either interrelated species or a
network of spatial locations, the techniques are suited to investigation of the same
phenomena in a general network setting. Throughout this chapter, we view the terms
network and *system* similarly – that is, as a group of entities or components that are
not independent (e.g., abundances of multiple species at different locations) and that
have linked or connected dynamics.

We emphasize that the focus of this chapter is on the use of time-series data
to draw inferences about ecological systems and networks. Use of these and other
approaches to inference should result in the development of models of ecological
systems. Such system models can then be analyzed using a variety of approaches
(e.g., graph theory) for purposes such as decomposition and identification of
compartments and subsystems [ABB06, CGC06] and identification of "important"
species [BJP09, JOBL08, Jor09].

2   System Identification

By system identification, we simply mean that we would like to use time series
from one or more state variables from a system of interest to draw inferences
about characteristics of the entire system. Ecological systems can contain large
numbers of potential state variables (e.g., populations of various species at different
locations in a spatially extended system), such that attempts to monitor all such
variables would be extremely difficult and expensive, at best, and more typically
impossible [MZSM04]. However, approaches from nonlinear dynamics offer hope
to the ecologist of being able to learn something about the dynamics of an entire
multidimensional system based on a time series of one or a few state variables. This
possibility causes us to consider the use of these same approaches to identify those
state variables that yield the greatest information about system dynamics.

A useful geometric description of dynamics for a multidimensional system is based on the concept of an *attractor*, which is a closed set of points in state space (e.g., defined by the abundance of each interacting species in the system). System trajectories beginning on the attractor remain on it, whereas trajectories beginning near (specifically, in the associated *attracting set*) the attractor will converge to it (for more precise definitions of attractor, see [Mil85, Str94]). The attractor is thus the portion of state-space in which the system tends to remain and to which it returns following perturbation. The geometry of an attractor thus contains a great deal of information about system dynamics. Indeed, ecological interest in a system's attractor is analogous to interest in stable equilibria for systems of multiple competing species [May73]. The strict definition of an attractor assumes that the underlying dynamics are deterministic. However, the concept of state-space can be quite useful with or without such an assumption. A state-space view of system dynamics provides the practitioner with a picture of the relative frequencies (probabilities) of the system's returning to a given state. Many of these geometric approaches are based on local probability density estimates (or closely related measures on an attractor; [ER95]) and/or the transition probabilities of moving from one location to another in the state space. This connection between geometric and probability density descriptions is important to the understanding of how attractor-based approaches to system identification can be applied to ecological systems. Thus, attractor-based methods may be appropriately viewed as a special subset of density-based approaches to time-series analysis. This view also blurs the distinction between approaches based on geometry versus information content.

The concept of an attractor is typically applied to stationary systems, such that the rules governing system dynamics are not changing over time periods of interest. If systems themselves are changing over a period of interest, then the concept of an attractor may no longer be useful. However, note that such change presents problems, not only for attractor-based approaches, but also for virtually any approach to the conduct of science. Science is based on predictions, and if systems change so rapidly that there is no basis for prediction (historic system dynamics provide no information about future dynamics), then there is little hope for doing anything other than describing change. A second comment concerns the possibility of using geographic replication to draw inferences about system attractors. The assumption of stationarity is needed for single time series to provide temporal replication or multiple looks at system dynamics as the system travels through state space. If multiple independent looks at system dynamics are provided by geographic replication, then systems need not be stationary for long periods to draw inferences about their respective attractors. However, we note again that learning about system dynamics during one time period may not be informative about future times if substantive changes in dynamics occur. Later in this chapter, we focus on detecting such change. Finally, we note recent work indicating that the concept of an attractor still provides a useful description for systems that experience specific kinds of change, for example systems subjected to either deterministic or stochastic forcing [SBDH97, Sta99, SBDH03].

Construction of an attractor for a multispecies ecological system appears to be a daunting task, requiring time series of abundances for each species in the system. However, Takens embedding theorem ([Tak81], also see [PCFS87, SY91, Whi36, Yul27]) provides an approach by which the attractor of a multidimensional system can be qualitatively reconstructed (such that the reconstructed attractor is diffeomorphic – geometrically equivalent – with respect to the original attractor) from a time series of data from a single system state variable (e.g., a single species). Specifically, delay coordinates of the single series are used to construct new pseudo time series from the original data. Reconstruction requires selection of the number of delay coordinates to use (the embedding dimension) and the length(s) of the delay [PMNC07, Wil97].

This basic approach to attractor reconstruction has been used successfully for long deterministic time series of single state variables from systems that are not of very high dimension. If time-series data from more than one system state variable are available, then delayed copies from multiple time series can be used in the embedding, again presenting an interesting optimization problem that requires selection of appropriate state variables and their respective delay copies [PMNC07].

Ecological time series are typically short and noisy, leading to the obvious question of what to do in this situation. In some cases, addition of noise obscures underlying determinism, whereas in other cases attractor-based approaches still provide reasonable inference about deterministic structure [SEK86]. This result anticipated the demonstration by Casdagli [Cas92] that attractor reconstruction also applies to input–output systems with stochastic input. It is likely that reasonable models of state variables of ecological systems will include deterministic components as well as term(s) representing the actions of exogenous variables that are modeled as random noise. Despite the existence of such random noise terms, Cheng and Tong [CT92] note that the search for low dimensional attractors is a meaningful signal extraction exercise.

3 Coupling and Comparative Dynamics

The preceding material involved efforts to draw inferences about an entire dynamical system based on the time series of one or more system state variable(s) [PMNC07]. In addition, we would frequently like to use two or more time series to address two general classes of problems. The first class involves investigation of interactions or coupling among state variables hypothesized to be components of the same system. Such investigations not only permit inference about the structure of ecological systems (e.g., nature and degree of interaction) but also address the ability to draw inferences about one system component by monitoring another. The second class of problem involves comparison of two time series, perhaps of the same system component, but from different locations or periods of time, to test for possible

differences in system dynamics. Such comparisons will be relevant to inferences about change in ecological systems, regardless of whether change is hypothesized to be associated with an identified perturbation.

3.1   Coupling

If two state variables are components of the same system, then they exhibit dynamical interdependence [PCH97, SSCBS96]. The existence of dynamical interdependence underlies the ability to reconstruct a system's attractor from a time series of a single state variable. Coupling between different biological state variables implies the existence of one of a number of kinds of interactions of substantial interest to ecologists. If different species are involved, then trophic (e.g., predator–prey, food web) or competitive interactions are suggested. For populations of the same species at different locations, active dispersal can result in dynamical interdependence. Linear cross-correlation has been used frequently by ecologists to investigate relationships between state variables, especially single species populations at different locations [BIL99, Koe99, KR02, PF02, RKL98]. Linear cross-correlation assumes a very specific functional relationship that is symmetric in its argument and defines coupling in terms of second-order correlations only, i.e., $E[x(t), y(t + T)]$, where $x(t), y(t)$ are the values of two state variables at time t. Here we consider methods that are based on the entire probability density structure (i.e., correlations of any order) and are therefore more generally applicable and capable of dealing with nonlinear systems. The methods we consider also lead to inferences about asymmetries between system components. These asymmetries can involve information and/or dynamical influence and are of great potential interest to ecologists [Njm05, NMNPC05].

Attractor-Based Approaches

Some methods for investigation of coupling are based on reconstructed attractors for each of the two state variables of interest. Continuity statistics are based on the fact that if two state variables belong to the same system, then their respective attractors must be related by a continuous function [MPNTW04, PCH95, PCH97]. Estimation of continuity between two system variables involves realizing the mathematical definition of continuity in an algorithm. To this end, one can use the algorithm developed in [MPNTW04]. This algorithm first focuses on a local region defined by a single fiducial point on one attractor (designated the source) and including its near neighbor points, and the corresponding neighborhood on the other attractor (designated as the target) defined by points with the same time indices as those on the source. The continuity statistic reflects the degree to which the points in the region on the source attractor map to a local region on the target attractor (indicating

greater likelihood of continuity) or are instead widely scattered across the target attractor (indicating smaller likelihood of continuity). Computations are based on a number of fiducial points across the source attractor, and inference is based on average values of these continuity statistics. Continuity statistics are not expected to be the same in both directions (i.e., when the roles of target and source attractors are reversed), reflecting any asymmetries in connectivity between the two system components.

Mutual prediction [SSCBS96] is another approach to investigation of coupling that is based on reconstructed attractors from two time series. The approach assesses the degree to which dynamics of one attractor can be used to predict the dynamics of another. If the two attractors indeed belong to the same system, then their dynamics should follow similar dynamical paths. A fiducial point is randomly selected from one attractor, and the neighborhood local to this point is selected from the other attractor. This neighborhood is based strictly on spatial proximity, and there is no necessary relationship between the time indices of the fiducial point and the points in the corresponding neighborhood on the other attractor. The trajectories of these neighborhood points are then used to forecast the dynamics on the original attractor, and the difference between predicted and actual dynamics provides a metric reflecting predictive ability. As with continuity, predictive ability is assessed for a large number of points across the attractor and an average value computed. Mutual prediction can in fact be used as a test for continuity [SSCBS96]. Both continuity and mutual prediction between attractors can be asymmetric, reflecting differences in information flow between system components.

This discussion has focused thus far on two state variables suspected to be components of the same system or network. We note here that it is also possible to build a multivariate attractor using information from multiple system state variables. It is then possible to use either continuity or mutual prediction to assess coupling of a single state variable and the multivariate reconstruction based on a number of other system components [NMNPC05].

These methods and others to be described in this section have seen little use in ecological settings; so we will illustrate some of them using time-series data generated from a two-species, spatially distributed, ecological model. The predator–prey model was introduced by Pascual [Pas93] and further explored by Little et al. [LEPNKSCS96] and Nichols et al. [NMNPC05]. The model describes system dynamics via dimensionless variables for predator (h) and prey density (p) along a one-dimensional spatial gradient, with location designated as x. System dynamics are specified as follows:

$$\frac{\partial p}{\partial t} = r_x p(1 - p) - \frac{ap}{1 + bp}h + d\,\frac{\partial^2 p}{\partial x^2},$$

$$\frac{\partial h}{\partial t} = \frac{ap}{1 + bp}h - mh + d\,\frac{\partial^2}{\partial x^2}h,$$
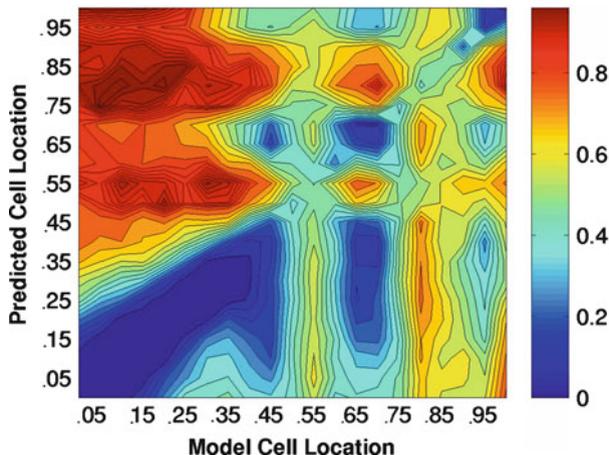
$$r_x = e - fx. \tag{8.1}$$

Fig. 8.1 Mutual prediction computed for predator–prey dynamics at different spatial cell locations of a spatially extended system (8.1), with prey resource gradient extending from low (cell $x = 1$) to high ($x = 0$) resources with resource slope parameter $f = 1.4$. Predator–prey data from one model cell location are used to predict predator–prey dynamics at another location (predicted cell location). Scaled predictive ability is indicated by color and ranges from high (0, *blue*) to low (1, *red*)

Reflective boundary conditions are assumed at $x = 0, 1$ with:

$$\frac{\partial p}{\partial x} = \frac{\partial h}{\partial x} = 0.$$

Parameters include predator–prey coupling a, prey-carrying capacity b, predator death rate m, diffusion coefficient d, and the intrinsic growth rate of the prey population r_x, which is a function of space and reflects a linear gradient in prey resource abundance. Some parameter values were fixed as in [Pas93], $m = 0.6$, $d = 10^{-4}$, $e = 5.0$, and $b = 2.0$. This model is continuous with respect to time and system state (predator and prey abundances are real-valued rather than integers), and will thus provide reasonable approximations in some situations and not in others [DS04]. However, we note that the methods we describe should be applicable to discrete time and/or state models as well. The spatial network of predator and prey density is particularly suited to the following methods that describe connections within the network of observed variables. To illustrate continuity and mutual prediction, the above described model was integrated for $n = 1,000$ time steps at spatial locations $x_i = 0.01, 0.02, \ldots, 0.99, 1.00$ using resource gradient slope of $f = 1.4$. The dynamics for lattice site x_i are given in state space by the vector $X_t^{(i)} = (P_t^{(i)}, H_t^{(i)})$. We assess both the mutual prediction (Fig. 8.1) and continuity (Fig. 8.2) metrics between state vectors $X_t^{(i)}$, $X_t^{(j)}$ $i, j = 0.01 \ldots 1.00$.

Both approaches are clearly capable of identifying asymmetries in the coupling among the various lattice sites. In general, there is stronger evidence of continuity
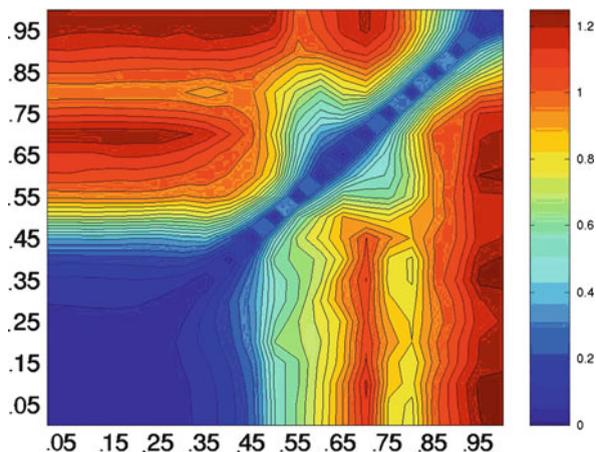
Fig. 8.2 Continuity computed for predator–prey dynamics at different spatial cell locations of a spatially extended system (8.1), with prey resource gradient extending from low (cell $x = 1$) to high ($x = 0$) resources with resource slope parameter $f = 1.4$. The continuity statistic reflects the function relating predator–prey dynamics at one location (source) to dynamics at another location (target). Scaled continuity is indicated by color and ranges from high (0, *blue*) to low (1+, *red*)

mapping dynamics at the low end of the resource gradient ($x = 1.00$) to those at the high resource end ($x = 0.00$) than vice versa. Similarly, the dynamics at the low resource end do a better job (on average) of predicting dynamics at the high resource end. By highlighting asymmetries in spatial coupling, these results suggest a possible monitoring strategy (see later discussion and Nichols et al. [Njm05, NMNPC05], Moniz et al. [MNN07]). The results in Figs. 8.1 and 8.2 are based on attractors reconstructed using the time series of both predator and prey state variables. However, if only data from a single-state variable are available, results of Takens theorem can be used to reconstruct the attractor using delay coordinates to obtain similar results [NMNPC05]. This possibility leads to interesting questions about optimal allocation of resources to monitoring programs (e.g., one or more species at one or more locations).

Information-Theoretic Approaches

Although attractor-based approaches are potentially useful in exploring coupling in dynamical systems, assessment of the direction of information flow is arguably ad hoc. Alternative approaches based on information theory have been recommended for the investigation of coupling, in part because such approaches involve formal characterization of the direction of information flow. Because these approaches have seen little use in ecology and because of our belief that they hold promise, we will describe two such information theory-based approaches in somewhat more detail than methods presented above (we discuss the joint utility of attractor-based and

information-theory approaches later). Let Y and Z represent two state variables reflecting two dynamical processes, and assume that we are investigating the possibility that they are coupled and actually components of the same system. We obtain simultaneous measurements of each system resulting in two time series, y_t and z_t, where $t = 1 \ldots M$ is a discrete time index. Each measurement is viewed as a discrete random variable with underlying probability distribution function $p(y_t)$ and $p(z_t)$, respectively, and joint probability distribution $p(y_t, z_t)$. The amount of information (in bits) about one state variable that is gained by knowing the value of the other variable is given by *mutual information* [VSw88, Wil97]:

$$I(Y, Z) = \sum_{y,z} p(y_t, z_t) \log_2 \frac{p(y_t, z_t)}{p(y_t) p(z_t)}. \tag{8.2}$$

Mutual information (8.2) is a Kullback entropy [Kul59] in that it reflects the excess information needed to encode $p(y_t, z_t)$ when erroneously assuming that the two variables are statistically independent [Sch00]. In order to compute mutual information, the probability distribution functions may be estimated using "bin counting" or other kernel density estimation approaches (e.g., see [Njm05, VSw88, Wil97]). The directionality of information flow or transport may be addressed by modifying the above expression for mutual information to include a time delay in one of the variables [Njm05, VSw88]:

$$I(Y, Z_T) = \sum_{y,z} p(y_t, z_{t+T}) \log_2 \frac{p(y_t, z_{t+T})}{p(y_t) p(z_{t+T})}, \tag{8.3}$$

where T indicates the delay. This quantity is referred to as time delayed mutual information. The investigator searches for the delay, $T_{\max}$, for which $I(Y, Z_T)$ is a maximum. $T_{\max} > 0$ suggests information transport from Y to Z, whereas $T_{\max} < 0$ suggests information transport from Z to Y. When the system of interest is characterized by a spatial component, and when Y_t and Z_{t+T} can be measured at different points in space, then the functional relationship between $T_{\max}$ and distance separating the two locations can even be used to draw inferences about the nature or form of the coupling function [VSw88, Njm05]. A more formal approach to inference about information flow was recently suggested by Schreiber [Sch00], who recommended a focus on state transition probabilities rather than on static probabilities. This approach, *transfer entropy*, considers systems that can be characterized as stationary Markov processes of specified order, k, where transition probabilities are denoted as $p(y_{t+1} \mid y_t, y_{t-1} \ldots y_{t-k+1}) = p(y_{t+1} \mid y_t^{(k)})$. The approach then considers another possible system state variable, Z, and asks whether knowledge of this variable provides additional information about the dynamics of Y. In the absence of information flow between Z and Y, the following equality should hold:

$$p\left(y_{t+1} \mid y_t^{(k)}\right) = p\left(y_{t+1} \mid y_t^{(k)}, z_t^{(l)}\right). \tag{8.4}$$

Transfer entropy, $T_{Z \to Y}$, is a Kullback entropy focused on the deviation of the system from the generalized Markov property (8.4), i.e., on the extent to which extra information about the dynamics of Y is provided by Z:

$$T_{Z \to Y} = \sum_{yz} p\left(y_{t+1}, y_t^{(k)}, z_t^{(l)}\right) \log_2 \frac{p\left(y_{t+1} \mid y_t^{(k)}, z_t^{(l)}\right)}{p\left(y_{t+1} \mid y_t^{(k)}\right)}. \tag{8.5}$$

Transfer entropy is not symmetric, as information flow can be much stronger in one direction than another.

As with attractor-based approaches, the above descriptions of time-delayed mutual prediction and transfer entropy considered two variables, but it is possible to develop multivariate analogs. For example, mutual information can be used to consider the additional information provided by one variable about the multivariate distribution of a number of other system variables [PT95]. Similarly, transfer entropy can be used to assess the additional information provided by one variable about the transition probabilities of a number of component state variables.

Perhaps the biggest drawback to information-theoretic approaches is that their estimation can be difficult. Estimation of probability densities from time-series data is generally challenging, as the results will often depend considerably on how the data are "binned." Kernel density estimates tend to provide good results and are used in most work on information-theoretic approaches (in this work as well). A good discussion of the estimation of both mutual information and transfer entropy can be found in [KS02]. In the cited work, the convergence of kernel-based estimators of both quantities is discussed. Of the two quantities, transfer entropy is the more difficult to estimate and no guarantees can be made regarding convergence. An alternative estimator of transfer entropy was proposed in [MK02] which purportedly works well for limited data. Reliable estimation will likely remain the core issue regarding implementation of information-theoretics in ecological applications for some time.

As an example of the potential utility of IT approaches, consider the predator–prey model of (8.1) for resource gradient slope of $f = 1.4$. Using the time-delayed mutual information, we might explore how information (e.g., about predator/prey abundance) moves or flows from one spatial location to another. Let $P^{x=0.96}$ denote the prey time series recorded at spatial location $x = 0.96$. Following the work of Vastano and Swinney [VSw88], we can examine $I(P^{x=0.94}; P_T^{x=0.96})$ to examine how information moves from one lattice site to the other. Figure 8.3 shows the time-delayed mutual information computed between time series from several lattice sites at various levels of spatial separation. The "target" lattice site was fixed as $x = 0.96$ for each case. As shown in the plot, the "source" lattice site varied between $x = 0.50$ and $x = 0.94$. Several observations can be made from Fig. 8.3. First, the dominant peak of the mutual information occurs for positive lags indicating that information is moving from the high resource end to the low resource end [FS86].

Fig. 8.3 Time delayed mutual information, $I(P^x; P_T^{x=0.96})$, for prey populations recorded at a target location ($x = 0.96$) and various other locations ($x = 0.70, 0.75, 0.80, 0.85, 0.90, 0.94$). Results based on the spatially extended predator–prey model of (8.1) with resource gradient characterized by slope $f = 1.4$
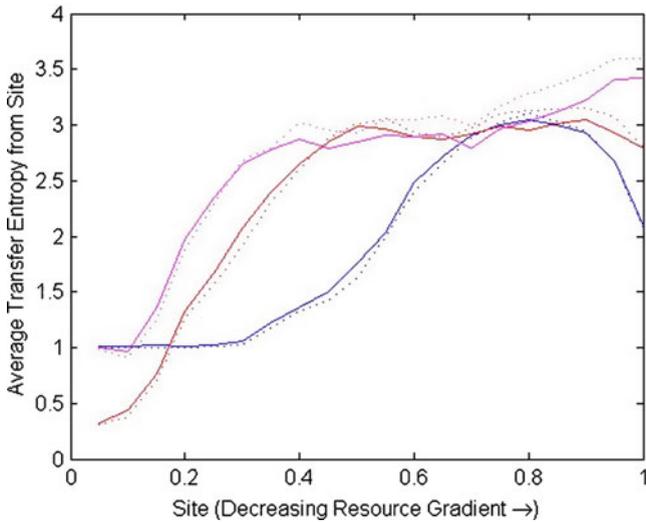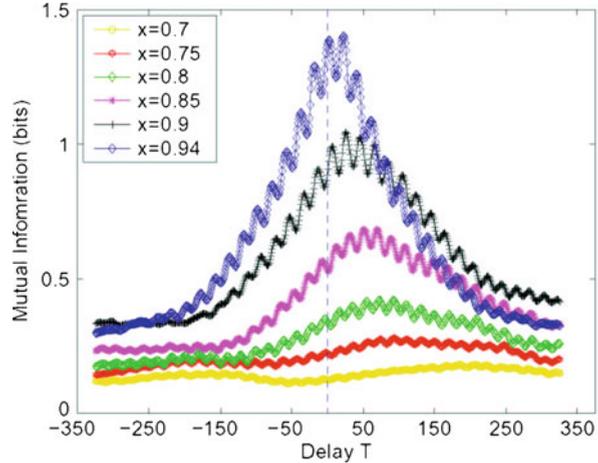

Fig. 8.4 Average transfer entropy from each site on the resource gradient to all other sites for three resource gradients, $f = 0.9$ (*blue*), $f = 1.4$ (*red*), $f = 1.9$ (*magenta*), where zero indicates high resources and one indicates low resources [model of (8.1)]. *Solid lines* indicate average $T_{\text{prey}\rightarrow\text{predator}}$, whereas *dashed lines* indicate average $T_{\text{predator}\rightarrow\text{prey}}$

In addition, the peak occurs at larger and larger lags as the degree of spatial separation increases (information takes longer to travel larger distances), providing inference about the speed of information transport, and thus the rate of prey dispersal [Njm05]. Similarly, we can use the transfer entropy to assess directionality of information transport. Figure 8.4 shows plots of average transfer entropy from each

site to all other sites for three values of slope of the resource gradient, $f = 0.9$, $f = 1.4$, $f = 1.9$ [see (8.1)]. The two plots for each slope show:

(1) The average $TE_{H^x \rightarrow P^{x'}}$, reflecting the extra information about prey transitions (averaged over all locations $x' \neq x$) provided by knowing the predator abundance at location x (*solid plots*).
(2) The average $TE_{P^x \rightarrow H^{x'}}$, reflecting the extra information about predator transitions (averaged over all locations $x' \rightarrow x$) provided by knowing the prey abundance at location x (*dashed plots*).

Two general comments emerge about information flow in this spatially extended predator–prey system. First, on average, more information about system dynamics is provided by knowledge of predator or prey abundance toward the low-resource end of the resource gradient. This result is consistent with the observations made previously using the continuity, mutual prediction, and mutual information metrics. Second, at locations near the high-resource end of the gradient, prey provide more information about predator dynamics than vice versa. Near the low-resource end of the plots, predators provide more information about prey, especially for the two steepest resource gradients, $f = 1.4$, $f = 1.9$. Results of this sort have clear implications for monitoring programs and concepts such as that of indicator species.

Combining Attractor-Based and Information-Theoretic Approaches

As noted above, inference about directionality of information flow based on attractor-based approaches is indirect, whereas the information-theoretic transfer entropy metric was developed specifically to assess directionality of information flow. However, transfer entropy does not always yield unambiguous inference either. For example, values of transfer entropy that approach zero [i.e., when $\frac{p(y_{t+1}|y_t^{(k)}, z_T^{(l)})}{p(y_{t+1}|y_t^{(k)})} \rightarrow 1$] can arise from two distinct situations [MNN07]. One possibility is that the two systems are unrelated, such that z_t is completely independent of y_t. The other possibility is that the systems governing z_t and y_t are identical, such that knowledge of y_t is equivalent to knowledge of z_t. In the latter situation, information about z_t may be useful in a monitoring context, whereas in the former case, information about z_t should not be useful. Moniz et al. [MNN07] have proposed the use of continuity statistics to resolve this ambiguity.

3.2 Comparative Dynamics

Methods for comparative dynamics focus on the detection of differences in dynamics of two systems based on two or more time series. Frequently, the question of interest will involve a single system that is observed for some initial period of time. Then, the system is perturbed, and, following a period of possible transient dynamics, a second time series is obtained. The question is whether the perturbation

has resulted in a change in system dynamics. The perturbation may be imposed experimentally or may instead involve natural phenomena. In some cases, the investigator may not identify a specific perturbation, but may instead be interested in possible damage or other changes that might occur as a system ages and is exposed to natural environmental variation. A number of questions about ecosystem change and damage are of interest to ecologists and natural resource managers. Both attractor-based and information-theoretic methods can be used to detect changes in system dynamics.

Attractor-Based Approaches

Attractor-based approaches such as mutual prediction and continuity statistics can be used with two time series of the same state variable, representing periods before and after some perturbation of interest. If long-term system dynamics remain unchanged following any transients produced by the perturbation, then the mutual prediction algorithm and continuity statistics should reflect similar attractor geometries, whereas changes in dynamics should lead to dissimilar attractor geometries. "Recurrence plots" [EKR97] were developed for the purpose of detecting and exploring nonstationarities in time series. They represent a graphical technique designed to highlight structure by focusing on the number of times that a system returns to a dynamical state. Assume a dynamical system comprised of r state variables, $\underline{x_t}$, that is directly measured at M points in time, $t = 1 \ldots M$ or obtained via attractor reconstruction. The recurrence matrix, R_{ts}(where s and t denote different points in time), is simply a matrix of 0s and 1s with entries defined as $R_{ts} = 1$ when $\underline{x_t}$ and $\underline{x_s}$ are close together (where "close" is defined as $\| \underline{x_t} - \underline{x_s} \| < \epsilon$, where ϵ is a threshold parameter and $\| \, . \, \|$ takes the Euclidean norm of the r-dimensional distance vector), and $R_{ts} = 0$ for $||\underline{x_t} - \underline{x_s}|| > \epsilon$. It was demonstrated in [RO2008] that the recurrence matrix can be related to a thresholded version of the local covariance matrix. The selection of the threshold ϵ will depend on the application. Too small a threshold and no recurrences will be visible (the plot will be all white except for the diagonal) while too large a threshold includes all points in the signal thus obscuring any structure present in the local covariance. A reasonable rule of thumb that has worked well in several applications is to take $\epsilon = 0.1\sigma$, where σ is the standard deviation of the time series.

Unlike continuity and mutual prediction, recurrence plots do not require preservation of the true underlying dynamics in the reconstructed attractor. Rather, recurrence plots simply allow the practitioner to visualize local covariances in the data as a function of time (for stationary, ergodic processes, summing R_{ts} over s and dividing by the number of data points, M, gives a probability density estimation of the system local to point "t"). Because recurrence plots are simply probing local density structure we do not have to faithfully reconstruct an "attractor" or even assume one exists.

Recurrence plots are always populated on the main diagonal and symmetric about it for constant ϵ. Analysis of recurrence plots is based on diagonal and vertical line

structures, where a line is defined as $l > 1$ adjacent points with no intervening white (nonpopulated) spaces [GC00, IB98, MWSK02, TGZW96]. Vertical lines reflect traditional ideas of autocorrelation, whereas diagonal structures reflect deterministic dynamics. Some kinds of purely stochastic dynamics (e.g., Gausian white noise) are characterized by the absence of structure, as nearby points at one time, t, have little chance of being neighbors again the next time, $t + 1$.

Recurrence plots can be modified to deal specifically with comparative dynamics of two processes, $x(n)$ and $y(n)$, by forming a cross-recurrence matrix [NTS06] based on the distance between points in the state space. With this approach, $CR_{ts} = 1$ for $\| \underline{x_t} - \underline{y_s} \| < \epsilon$, and $CR_{ts} = 0$ for $\| \underline{x_t} - \underline{y_s} \| > \epsilon$. In the case of cross-recurrence plots, line structures relate to the probability that the two systems obey the same dynamics. In the case of ecosystem change, the two processes could represent the same state variable(s) before and after a perturbation.

Recurrence quantification analysis [WZ94] refers to the computation of various summary statistics from recurrence and cross-recurrence plots or matrices. For example, percent recurrence is the percentage of darkened points in the plot, whereas percent determinism is the percentage of darkened points occupying significant line structures, where significant is often just taken to mean two or more adjacent points. These statistics can then be compared for recurrence plots made from time series before and after a perturbation, or statistics can be computed directly for the cross-recurrence plots based on the two time series.

As an example, again consider the predator–prey model described in (8.1). Figure 8.5 shows recurrence plots generated from the prey dynamics at spatial locations 0.13 (upper plot) and 0.96 (lower plot). Both plots were generated using a recurrence length scale of $\epsilon = 0.1\sigma$ where σ is the standard deviation of the time series. The dynamics at location 0.13 are largely periodic, hence the banded structure of the recurrence plot. The period of the oscillation corresponds directly to the spacing between the bands. Prey dynamics at location 0.96 are chaotic [Pas93] and exhibit a more complicated recurrence (probability) structure. If the diffusion constant d is modified to include temporal fluctuations, then a very different recurrence structure emerges. Letting $d(t)^* = d + 5(10^{-5\sin(2\pi g t)})$, where $g = 0.001$ samples/unit time (slow periodic modulation of diffusion coefficient), one sees different recurrence patterns (Fig. 8.6). The continuous, periodic bands at lattice site 0.13 are replaced by wavy patterns that are clearly being modulated by the time dependency in the diffusion term. The local probability density structure at lattice site 0.96 is also altered by the influence of d^*. However, in this case the complexity of the original recurrence plot makes it difficult to detect the influence of the nonstationarity in the diffusion term. This simple example illustrates the types of changes that can be observed when examining recurrence structure in time series data.

Information-Theoretic Approaches

Time-delayed mutual information and transfer entropy were described above as methodological approaches for the detection of coupling and information flow
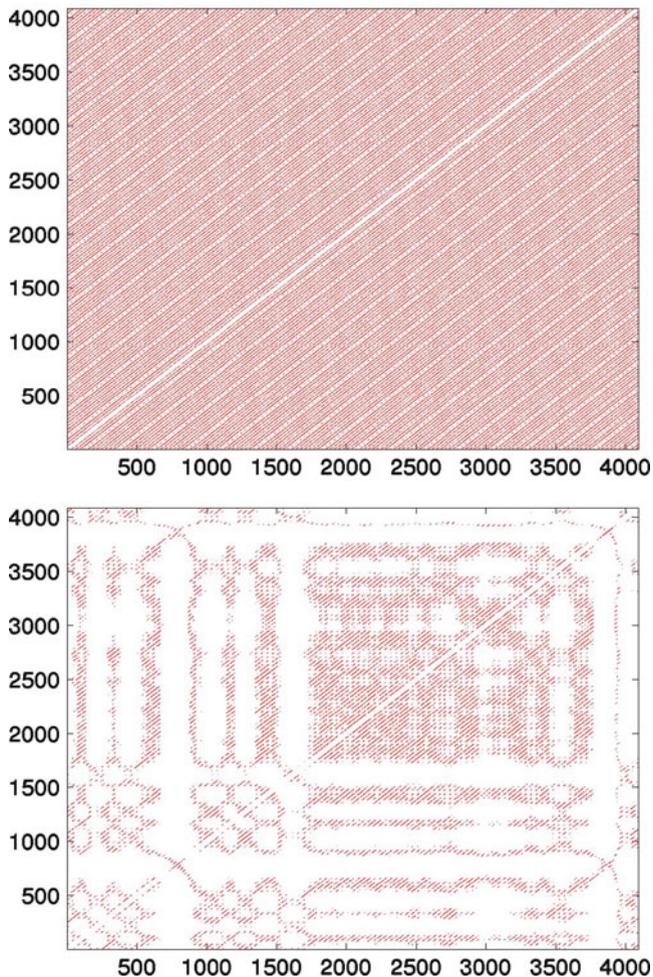
Fig. 8.5 Recurrence plots (both axes reflect time) of prey dynamics at spatial location 0.13 (*upper*) and location 0.96 (*lower*) along a spatial resource gradient from high (0) to low (1) prey resources. Recurrence length scale is $\epsilon = 0.1\sigma$, where σ is the standard deviation of the time series. Dynamics are based on the predator–prey model of (8.1), with constant diffusion coefficient, d

between system components. Non-transient changes in system dynamics following a perturbation to the system should be reflected in changes in coupling and information flow among system components. In the case of ecological monitoring, the two state variables or components might be two different species at the same location(s) or the same species at two different locations that are sufficiently close to be dynamically interdependent (see [Njm05, NMNPC05]). The approach to change detection would involve computation of time-delayed mutual information or transfer entropy for two system components during the period before, and then following,
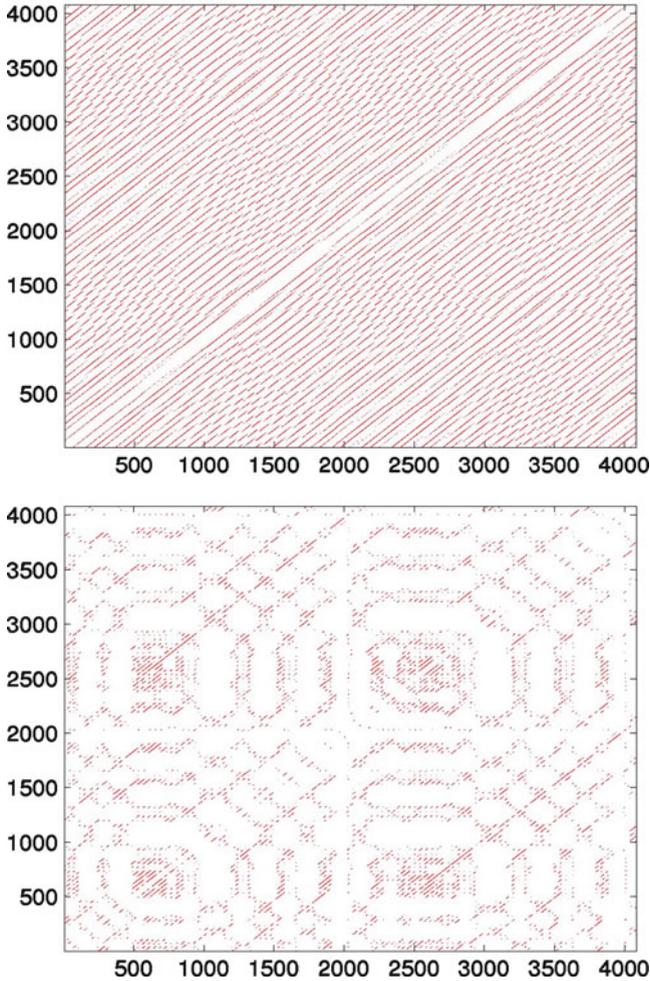
Fig. 8.6 Recurrence plots (both axes reflect time) of prey dynamics at spatial location 0.13 (*upper*) and location 0.96 (*lower*) along a spatial resource gradient from high (0.00) to low (1.00) prey resources. Recurrence length scale is $\epsilon = 0.1\sigma$, where σ is the standard deviation of the time series. Dynamics are based on the predator–prey model of (8.1), with diffusion coefficient varying temporally according to $d(t)* = d + 5(10^{-5\sin(2\pi gt)})$, where $g = 0.001$ samples/unit time (slow periodic modulation of diffusion coefficient)

a perturbation, where the post-perturbation data come after a delay to allow for transient dynamics. Differences in these metrics would reflect changes in system dynamics, whereas similarities would indicate an absence of change, at least with respect to the selected system components.

This section on comparative dynamics has focused on the comparison of one or more time series at two different times (e.g., before and after a perturbation).

We view this approach as potentially the most useful in assessment of ecosystem change. However, we also note that comparative dynamics may sometimes involve comparison of observed dynamics with that expected under a null hypothesis of interest. For example, Nichols et al. [NSTSP06] have proposed the use of the described information-theoretic approaches for damage detection in the field of structural health monitoring. One approach to this problem would be to compare a structure before and after the occurrence of suspected damage. However, [NSTSP06] note the advantages of being able to assess damage in the absence of baseline or pre-damage data. They equate nonlinearity with damage and then test for nonlinearity as a means of testing for damage. Specifically, they take time series of two system components from a structure that may be damaged (in their case, sensors placed at two different locations on the structure). They then create surrogate data sets from these original data sets that retain the exact linear cross correlation between the two measured variables. However, randomization is used to destroy higher-order correlations that may exist, thus producing surrogates that represent the null hypothesis of linearity. Comparison of this null hypothesis with the alternative of nonlinear dynamics is accomplished using time-delayed mutual information and transfer entropy, and damage (nonlinear coupling) is readily detected using this approach [NSTSP06]. The relevance of this approach depends on the reasonableness of equating nonlinearity and damage. This view of damage as nonlinearity is very common in engineering applications, but is also held by some in ecosystem thinking [Patt75].

4 Surveillance Monitoring and Information Extraction

In the following discussion, we return to the theme that the described methods of extracting information from time-series data form the basis of a conceptual framework for surveillance monitoring. We provide a linkage between the described methods and ecological inquiry, considering topics and questions of interest to ecologists, and suggesting specific methods that may be useful in addressing them.

4.1 System Identification

Ecological systems represent "enormously complex associations of species which interact in diverse ways. As a matter of practical necessity, field ecologists can rarely specify, much less quantify, all of the interactions" ([Sch81], p. 383). In the face of such unknowable complexity, ecologists have chosen to monitor the dynamics of one or a few species in hopes of learning something about the entire system. As noted above, Takens [Tak81] embedding theorem (also see [Yul27, Whi36, PCFS87, SY91, OY03, PMNC07]) provides a theoretical basis for

such hopes by demonstrating the possibility of learning about the dynamics of an entire system using a time series of data from a single (or small number of) system state variable(s).

We noted that attractor reconstruction using delay coordinates provides a geometric representation of system dynamics that provides information about the portions of state space in which we expect to find the system most of time. Such reconstructions also provide a basis for computing metrics (e.g., mutual prediction, continuity) for inference about coupling of system components.

4.2   Indicator Species

Ecologists have long recognized that presence or dynamics of a single species or group of species can be used as indicators of both physical and biological characteristics of systems in which they are found ([Odu71] and references therein). This recognition has evolved to the point where "indicator species" have become a central concept in ecological monitoring. The basic premise is that monitoring all system components is impossible for all but the simplest systems; so some selection of components to monitor is required [MZSM04, Sim98]. The literature of ecology and conservation biology contains many discussions of indicator species including such topics as a rationale for their use, methods for their selection, and criticisms of the concept [LVT88, MZSM04, Nos90, Noo03]. Noon ([Noo03], p. 43) specifies that indicator species should "provide information on the state of the unmeasured resources and processes of the focal ecological system", and emphasizes that "the ultimate success or failure of the [monitoring] program may be determined by this one step."

We believe that Takens [Tak81] theorem provides a theoretical justification for the concept of indicator species, insofar as it demonstrates the potential for time series of a single species to be used to reconstruct ("indicate") the dynamics of the system over the entire state space. Furthermore, the described methods for assessing coupling and dynamical interdependence provide a natural framework for considering indicator species as well as objective approaches for their selection. Both attractor-based methods (continuity and mutual prediction) and information-theoretic methods (time-delayed mutual information and transfer entropy) can provide asymmetric estimates of coupling, reflecting differences in information flow between either two measured system components or between one system component and a multivariate set of other components. The general work of Pecora et al. [PMNC07] on selection of time-delayed versions of system state variables for attractor reconstruction is very relevant to the selection of a set of indicator species that provides the most information about the dynamics of the entire system. For model systems designed to mimic real-world ecosystems, single state variables could be investigated one at a time for their information content with respect to dynamics of the entire system. Such an exercise could, for example, provide

general inferences about trophic level (our example use of transfer entropy for a predator–prey system) or other characteristics (e.g., generalists or specialists) of species having relatively high and low information content. The methods can also be used, or adapted for use, with actual monitoring data for example systems to provide inferences about which monitored species is providing the most information about the studied system. It would also be possible to compute the loss in information incurred by eliminating species from a list of those monitored. We believe that transfer entropy may hold the greatest promise for the investigation of indicator species, although we certainly do not rule out any of the described approaches that focus on coupling.

4.3   Species Interactions

The discipline of community ecology focuses on interactions between pairs of species. Trophic interactions, competitive interactions, and mutualistic interactions are all of interest to ecologists, yet they are not always readily observable. In some situations, it may be useful to pose questions about dynamically important interspecific interactions using time-series data from monitoring programs [IDCC03]. The described methods for investigation of coupling may be useful in such situations. Time series of two species suspected to interact can be investigated using attractor-based (continuity statistics, mutual prediction) or information-theoretic (mutual information, transfer entropy) approaches. Resulting inferences about coupling will be indicative of either dynamic interactions or dynamic responses to the same driving variable, a dichotomy that can be resolved in some cases using approaches such as transfer entropy and time-delayed mutual information [Njm05]. Asymmetric interactions between species are especially relevant to some ecological hypotheses [VSi02], and the ability of the described methods to detect and quantify asymmetric coupling will thus be useful. Initial efforts to draw inferences about simple food web structure based solely on time-series data from web components have been encouraging [MCENN07].

4.4   Spatial Coupling, Population Synchrony, and Spatial Sampling

In addition to investigating possible interactions among different species at the same locations, ecologists are interested in possible coupling of populations of the same species at a network of different spatial locations. Time series of monitoring data from different locations are frequently used to draw inferences about population synchrony [BIL99, CS03, Caz04, Koe99]. When evidence of such synchrony is found, two general classes of underlying mechanisms are typically

considered [BIL99, Koe99, RKL98, Njm05]. One involves active dispersal, with animals moving between locations. The other possibility involves response to a common environmental driver [Mor53].

Both attractor-based and information-theoretic approaches have been shown to be useful in assessing spatial coupling using time series generated from a spatially extended predator–prey model. Nichols et al. [NMNPC05] used both continuity and mutual prediction statistics to detect coupling and to draw inferences about its relative magnitude. Asymmetric spatial coupling was observed and was interpreted in terms of a prey resource gradient, and resultant spatial variation in dynamics. A comparison of these results with results based on linear cross-correlation led to the conclusion that the nonlinear approaches were superior for this model system. Nichols [Njm05] then used time-delayed mutual information with this same model system to draw more formal inferences about information flow between spatial locations within this system. He was further able to reject the hypothesis that a common environmental driver was responsible for the interdependent dynamics and even drew inferences about the nature of the dispersal functions responsible for the coupling [Njm05]. Mutual information has been used in conjunction with surrogate data sets to detect population synchrony in two-patch model systems and in actual data sets [CS03, Caz04].

In addition to investigating the factors responsible for dynamics of spatially extended ecological systems, these methods should be useful in providing insight into the relative value of different spatial sampling designs. Despite the abundance of work on static designs for spatial sampling [Tho02], there has been relatively little consideration of designs for sampling dynamical systems that exhibit variation over both time and space (see [MNN07, WR99] for exceptions). Stated differently, whereas ecologists have expended much effort discussing the concept of indicator species, there has been little attention devoted to consideration of possible indicator locations, locations that provide maximum information about dynamics of the system. As we noted, it is possible to use mutual information and transfer entropy to directly assess the information flow between multiple state variables (e.g., the abundances of a species at multiple locations within a system) and a single state variable (e.g., abundance of one species at one location) and vice versa [MNN07].

It is possible to use these methods on data from model systems with resource gradients or gradients in abundance, to try to gain insight into the characteristics of locations that provide most information about system dynamics. For example, the results presented above for the spatially extended predator–prey system based on the four different coupling metrics (continuity, mutual prediction, time-delayed mutual information, transfer entropy) indicated greater information flow from locations of high to low prey resource abundance than vice versa, a result consistent with the greater number of dispersers going from areas of high abundance and resources to areas of low abundance and resources [NMNPC05, Njm05]. This flow of information leads to an asymmetry in the information content of time series from different locations, such that low-resource locations provide more information about high-resource locations than vice versa (Figs. 8.1–8.4). This general inference based on multiple locations and different resource gradients is consistent with the recent

result of Jonzen et al. [JRP05] that in source-sink systems (sensu Pulliam [Pul88]), with dispersal from the source location to the sink but not vice versa, it is often most efficient to monitor the sink habitat. These results lead to the natural, yet henceforth unexploited, suggestion that asymmetric dispersal may be an important determinant of information content of monitoring data from various locations in ecological systems (also see [MNN07]).

It may also be possible to directly determine the most information-rich locations using data from spatially extended monitoring programs. Of course, the sampling design problem can be treated more generally as one of finding the species-location combinations that provide the most information about system dynamics (see [NMNPC05]). This combination of ideas about indicator species and spatial sampling points to a potentially productive approach of treating surveillance monitoring as a joint optimization problem.

4.5 Environmental Drivers

Our discussion thus far has focused on coupling between system components, whereas we are also frequently interested in environmental variables that may drive system dynamics. Pascual and Ellner [PE0] have developed approaches for identifying the driving variable from a set of candidates using time series of both potential drivers and system state variables. They focused on the period of the environmental driver and noted that more general approaches should be possible. All of the methods described above for assessment of coupling should be useful for this purpose.

The information-theoretic approaches seem especially well suited for identification of environmental drivers, and indeed Nichols [Njm05] identified a periodic driver for a model predator–prey system using mutual information. Cazelles [Caz04] has used information-theoretic approaches in conjunction with symbolic dynamics and the generation of surrogate data to investigate coupling in ecological time series. He demonstrated superiority of this approach to linear cross-correlation in model systems. He also used the approach successfully with actual ecological time series and found evidence of an association between sheep abundance on the island of St. Kilda and the North Atlantic Oscillation index, a composite environmental variable [Caz04].

4.6 Assessment of Ecosystem Change and Damage

Ecologists are frequently interested in comparing time series of state variables collected before and after some perturbation of interest (e.g., environmental change, management action) and even during two time periods not separated by some discrete event. The question is simply, have system dynamics been altered or do they

remain the same in the two periods? Mutual prediction provides one approach to investigating change, as prediction from one attractor to the other should be possible only if the system dynamics in the two time periods remain similar. Similarly, recurrence plots for the two time series should differ if dynamics have changed.

Another approach to detection of change involves the assessment of coupling between two state variables before and after the perturbation. Changes in system dynamics are reflected in changes in coupling of system components. Indeed, engineers place multiple sensors on structures and use evidence of changes in coupling between locations to detect damage in structural health monitoring [NNTSTV04]. Thus, we can envision using either attractor-based or information-theoretic approaches to assess coupling between two state variables before and following a perturbation.

Finally, we noted above that sometimes the described methods can be used with a single time series, or with time series of two state variables from the same time period, to draw inferences that may be relevant to change or damage. Recurrence plots have been used to detect nonstationarity of time series, and this approach could be used with ecological data, as in the above predator–prey example. It was also noted above that structural damage is frequently equated with nonlinear responses to vibration. It is thus possible to generate surrogate data for two coupled time series under the null hypothesis of a linear relationship, and to test this against the alternative of nonlinearity [NTS06]. Some ecologists view nonlinearity as a signal of ecosystem damage [Patt75], although we doubt that this will generally be true. However, if the distinction between damaged and undamaged is better captured by some other contrast in dynamical pattern, it may be possible to design surrogates that reflect other null hypotheses for testing [SS2000].

5 Summary

We began this review with three basic observations. First, ecological monitoring programs are of two basic types with respect to design and methods of analysis: hypothesis-driven programs developed for the conduct of science or management and surveillance programs developed as general sources of ecological information. Second, many ecological monitoring programs in place today are best characterized as surveillance monitoring. Third, virtually all of the methodological development associated with monitoring program design and data analysis has occurred for hypothesis-driven programs, with little quantitative attention having been devoted to surveillance monitoring. In this review, we have viewed the analysis of data from surveillance monitoring programs as an exercise in information extraction and as a specific example of the more general problem of determining interactions, information flow and synchronization from observations of an ecological network.

We have reviewed methods developed primarily in other disciplines for analyzing time series and suggested that they provide a natural methodological framework for surveillance monitoring programs. In some cases, the methods provide an upper

limit to what can be learned from time-series data. In other cases, they can be used with ecological models to design surveillance monitoring programs. We believe that such investigations hold promise for possibly drawing general inferences about information content of monitoring data from different classes (e.g., trophic levels) of species and different locations characterized by different levels of immigration and emigration. We also believe that work with model systems can be used to explore the idea of surveillance monitoring design as a joint optimization problem involving both species and space. Finally, in still other cases the methods described in this review should be directly useful for analysis of certain kinds of ecological data.

Some of the described methods can be used in the general process of system identification. Other methods are useful for identifying important environmental drivers and for assessing the strength of species interactions. If multiple locations are monitored, then spatial coupling of populations can be identified, and general inferences about dispersal are even possible. Some methods are well suited to investigating possible changes in long-term system dynamics occurring either generally over time or in association with an identified event.

The attractor-based approaches discussed above were developed for long time series (many thousands of points) from deterministic systems, whereas the information-theoretic approaches appear to be more flexible and widely applicable. Three practical issues that arise when considering application of these methods to ecological time series are short series lengths, stochasticity, and stationarity. We believe that much can be learned from model systems for which none of these issues should be a problem. In addition to such exercises, time series can be generated from models, and the relevance of stochasticity and series length to inferences resulting from the described methods can be directly assessed. Recent efforts of this type have been encouraging, with information-theoretic approaches being useful with short time series and in the presence of stochasticity [MCENN07]. Several approaches are available for assessing system stationarity and have been used for identifying ecological time series appropriate for the analyses described herein [MNN07].

Nevertheless, for actual ecological monitoring data, much work remains. With respect to series length, some ecological time series (e.g., meteorological variables such as air temperature and wind speed, water levels in certain systems) are sufficiently long for attractor-based approaches [KSE04, MNN07]. Time series of animal abundances do not tend to be nearly long enough for some of the described approaches, and the likely solution involves more specific parametric modeling [ET95, TE00] than is necessary for long series. The use of null hypothesis surrogate data sets has also proven useful with short data sets arising in ecology and other disciplines [CS03, Caz04, MK02]. With respect to the issue of determinism and stochasticity, the recent assessment of Schreiber ([Sch00], p. 3) seems relevant. "Neither naive enthusiasm to explain all kinds of unsolved time-series problems by nonlinear determinism is justified, nor is the pessimistic view that no real system is ever sufficiently deterministic and thus out of the reach for analysis. At least, chaos theory has inspired a new set of useful time-series tools and provides a new language to formulate time-series problems – and to find their solutions."

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