Extending Nonlinear Analysis to Short Ecological Time Series

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ABSTRACT: Nonlinearity is important and ubiquitous in ecology. Though detectable in principle, nonlinear behavior is often difficult to characterize, analyze, and incorporate mechanistically into models of ecosystem function. One obvious reason is that quantitative nonlinear analysis tools are data intensive (require long time series), and time series in ecology are generally short. Here we demonstrate a useful method that circumvents data limitation and reduces sampling error by combining ecologically similar multispecies time series into one long time series. With this technique, individual ecological time series containing as few as 20 data points can be mined for such important information as (1) significantly improved forecast ability, (2) the presence and location of nonlinearity, and (3) the effective dimensionality (the number of relevant variables) of an ecological system.

Keywords: dimensionality, nonlinearity, forecasting, S-map, composite time series, dewdrop regression.

Ecological systems often show erratic ups and downs and can appear to shift abruptly from one state to another (Holling 1973; Scheffer et al. 2001; Scheffer and Carpenter 2003). Simple linear or equilibrium models do not capture this kind of behavior, but it is the hallmark of mathematical systems governed by nonlinear dynamics (May 1977; Prigogine 1984; Bak et al. 1987; Hastings and Sugihara 1993). These dynamics appear ubiquitous in terrestrial (Ludwig et al. 1978; Schaffer 1984; Dublin et al. 1990), freshwater (Carpenter et al. 1999), and marine systems (Sutherland

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1974; Dixon et al. 1999; Hare and Mantua 2000; Knowlton 2004; Hsieh et al. 2005b). However, linear and equilibrium models are still used to describe fisheries (e.g., maximum sustainable yield) and managed terrestrial ecosystems, perhaps because nonlinearities typically are challenging to identify and hard to mathematically characterize and validate.

The difference between fluctuations caused deterministically by low-dimensional nonlinear dynamics and those caused stochastically by high-dimensional linear noise has far more than academic interest; it is fundamental to understanding and modeling ecosystems (Sugihara and May 1990; Sugihara 1994; Pierce 2001; Rudnick and Davis 2003; Mantua 2004; Hsieh et al. 2005b). For example, if it can be shown that a system is governed by a dominant low-dimensional nonlinear mode (i.e., where most of the ups and downs can be explained by a few variables interacting in complicated ways), then in principle it should be possible to construct a simple mechanistic model that captures this behavior. Because such a model requires few inputs, monitoring those input variables in a real ecosystem will presumably be feasible and inexpensive. This will not be possible if it is found that the underlying system is predominantly high dimensional or linear-stochastic (involving the additive action of many variables). In this case, mechanistic modeling will be difficult because of the large number of variables involved, and the best strategy may be implementing a statistical, phenomenological autoregressive (AR) model. Therefore, identifying whether the dynamic contains a dominant low-dimensional mode or is essentially linear-stochastic is a fundamental first step toward understanding how to model ecological systems.

Unfortunately, the data required to make these determinations with existing nonlinear time series techniques are often prohibitive. Because of the need for lengthy time series, these methods cannot be used in most ecological studies. Although nonlinear ecology is a wide and active field and many breakthroughs have been made (e.g.. Ludwig et al. 1978; Schaffer and Kot 1986; Bolker and Grenfell 1993; Hastings et al. 1993; Grenfell et al. 1994, 1998; Higgins et al. 1997; Bjornstad and Grenfell 2001 and references therein), important information such as dimensionality and predictability remains unknown for most ecosystems.

Here we present a practical technique that allows measurement of the nonlinearity and dimensionality of relatively short time series, with a consequent increase in our understanding of the dynamics and an increase in forecast skill.

The Simplex Projection and the S-Map: Nonlinear Analysis of One Long Time Series

Standard methods for determining the dimensionality and nonlinearity of the hidden process that gives rise to a time series use state-space reconstruction with lagged coordinate embeddings (Takens 1981). This reconstruction procedure is a way of creating a shadow version of the attractor (motion vectors or phase space) governing the original process, from time series observations on a single variable in the process (e.g., the time series of abundance of one species in a multispecies ecosystem can be used to model the whole system). To embed such a series of scalar measurements, vectors in the putative phase space are formed from time-delayed values of the scalar measurements: $\mathbf{x}_t = \{x_t, x_{t-\tau}, x_{t-2\tau}, \ldots, x_{t-(E-1)\tau}\}$, where t is time, E is the embedding dimension, and τ is the lag (see Sugihara and May 1990 for the choices of E and τ). Takens's theorem states that the shadow version of the dynamics reconstructed by such an embedding preserves the essential features of the true dynamics ("topological invariants"). That is, even if a species' abundance through time depends on variables that were not measured, we can still reconstruct a shadow that accounts for these missing variables by taking the E prior values from just one species as a coordinate in E-dimensional space. This reconstruction can require large amounts of data, especially if the underlying dimensionality is high (Ruelle 1989; Tsonis 1992).

Two techniques built on this theory are the simplex projection method (used to determine dimensionality; Sugihara and May 1990) and the S-map procedure (used to detect nonlinearity of the time series; Sugihara 1994). The simplex projection and S-map methods are well documented, have been described elsewhere (Dixon et al. 2001; Landini et al. 2002; Ito and Ito 2005), and are briefly summarized in appendix A in the online edition of the *American Naturalist*. Note that neither method "fits" equations to data; rather, they rely on a set of data to forecast a second out-of-sample set not used in model construction. Typically, the first half of the time series (library set) is used to build the model, and the second half (predicted set) is forecast as output, often with stunning accuracy (Sugihara and May 1990). This robust out-of-sample forecast procedure, called cross-validation, avoids overfitting. A portal for the simplex projection and S-map is available online (http://www.iod.ucsd.edu/simplex/).

After some initial confusion regarding implementation

of these techniques was resolved (Sugihara 1994), ecologists have made them among the most commonly used nonlinear predictive tools in the literature. Nonlinear science is a very broad area of mathematics in general, and quantitative ecology in particular, and there are many techniques for detecting nonlinearity and for fitting nonlinear curves to data (fuzzy logic, generalized additive models, state-space models, genetic algorithms, neural networks, kernel density estimators, etc.). If we limit our attention to the specific goal of creating appropriately dimensioned predictive models from nonlinear time series, a few other alternatives exist. Local Lyapunov exponents were tentatively proposed as a way of detecting chaos and instability while controlling for noise in the data (Ellner and Turchin 1995; cf. Sugihara 1994 for a critique of this method), though the technique was later altered (Turchin and Ellner 2000) to be surprisingly similar to the S-map (models are selected by cross-validating forecasts made from an atlas of lagged coordinate embeddings smoothed through an exponential kernel). Recently, several articles have demonstrated low dimensionality in marine ecosystems, using recurrence analysis (e.g., Royer and Fromentin 2006; King et al. 2007). This interesting technique is also based on lagged coordinate embedding and is useful in visualizing patterns in the data and determining dimensionality of the system. However, it involves fitting as opposed to prediction and consequently does not make forecasts, nor does it quantify the degree of nonlinearity in a system.

Dewdrop Regression: Nonlinear Analysis of Several Short Time Series

Description of the Technique and Theoretical Justification

Failure to identify and understand nonlinearity has been singled out by many prominent ecologists as the single largest barrier to understanding ecosystem processes (Levin 1992, 2006; Scheffer et al. 2001; Knowlton 2004). However, simplex projection and the S-map have failed to become standard fare in their native discipline for the simple reason that they require time series that are quite long, and ecological time series, generally, are not. As we show, this limitation can be overcome when data from several sufficiently equivalent species are available (e.g., different fish species in the same geographic region). A composite time series can often be constructed to make a longer time series, so that standard nonlinear forecasting methods apply. A preliminary version of this idea was suggested for analyzing equivalent cardiac rhythms from short electrocardiogram tracks (Sugihara et al. 1996). However, there is an ecological rationale behind constructing a composite time series that relates to the original embedding article by Takens (1981).
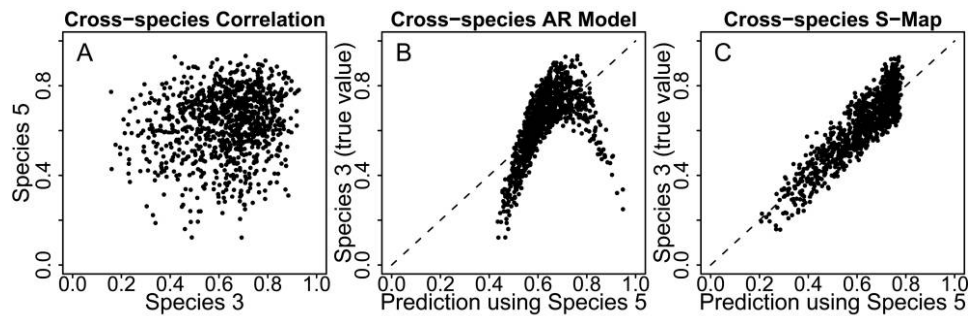
Figure 1: *A*, In our noisy five-species competition model, there was no clear temporal relationship between species (species 3 and 5 were chosen randomly as representatives). *B*, Predictions of species 3 abundance, using a linear model constructed from species 5, had systematic errors. *C*, However, nonlinear predictions were accurate across the entire range of abundance.

Any dynamic system (e.g., an ecosystem) generates a vector field (*N*-dimensional phase space); if the system is dissipative, then the vector field collapses to a geometric shape (an attractor) in dimensions lower than the original dynamics would suggest. This attractor characterizes the dynamics (e.g., fluctuations in populations) as they occur in the space of relevant variables (state space). For example, Schaffer's (1984) pioneering work suggested that an attractor embedded in three dimensions could characterize lynx and hare populations. This attractor had a funnel-like shape in his particular three-dimensional embedding. Conversely, each species' time series of abundance is a one-dimensional "shadow" of paths across the multidimensional attractor of the ecosystem. Insofar as each species is ecologically similar, each time series can be regarded as a similar, possibly rescaled, observation of the same ecosystem attractor. In this case, the shadow of one species can be rescaled and used to predict the time series of an equivalent species, using embedding techniques. This is true even if one is more abundant than the other and even if the species peak at different times. Species with dynamically equivalent time series see the same attractor geometry, though possibly from different points of view and possibly at different scales.

However, be aware that not all species have equivalent time series. Ecologically different species see the attractor from different angles and potentially could see a different geometric shape. One can think of a species' niche as determining the angle from which the attractor is viewed, which in turn determines the time series. In other words, a three-dimensional path across an attractor will cast a different one-dimensional shadow (time series) depending on the angle from which it is viewed. Unless the attractor appears similar from both points of view, the time series will not be equivalent and cannot be used to forecast each other. Ecological differences should be taken into consid-

eration when selecting time series for compositing. We later describe a quantitative method to identify dynamic equivalence (the "similar shadow" test). We have also developed a method for dealing with dynamically distinct time series that will be discussed in a separate article (C. N. K. Anderson, C.-h. Hsieh, and G. Sugihara, unpublished manuscript).

A time series of population abundances can be generated from a discrete time growth model by simple iteration (a process sometimes referred to as "cobwebbing"). Here we face the opposite problem: extracting a growth model from the time series of abundance. By embedding each short time series, a few points appear on the surface of the attractor, like dewdrops on a cobweb. The more series we use, the more dewdrops appear and the more detailed our image of the attractor becomes; ergo, we propose naming this technique "dewdrop regression."

A Model Example

We simulated a five-species competition model with chaotic dynamics and process noise (app. B in the online edition of the *American Naturalist*), creating long (*N* = 1,000) time series of the abundance of each species. Although each species interacted with all others (they were deterministically coupled), their time series appeared unrelated temporally (fig. 1*A*). This shows that the lack of any statistical (linear) relationship between variables does not preclude the existence of a deterministic relationship between them. We also used an autoregressive model (AR4) to look for linear relationships outside of the temporal domain (linear cross-predictability between species). The AR model had systematic errors only slightly smaller than the standard deviation in the time series data, indicating predictive power that is on average no better than the mean value (table B1; fig. 1*B*). We note that the AR4
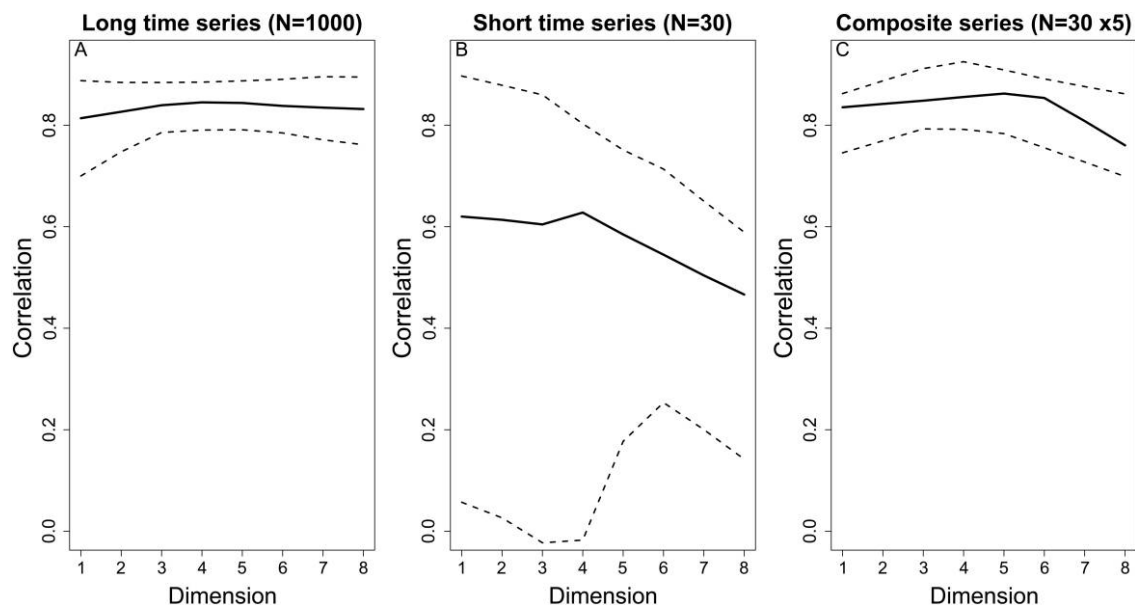
Figure 2: *A,* In our noisy five-species competition model, 15 points could be accurately predicted from a library of 985 with simplex projection (bootstrapped 1,000 times). It appears that our model is effectively four-dimensional, and this is shown clearly in the 95% confidence limits (*dashed lines*). *B,* Predicting 15 points using a short library to 15 points greatly reduced predictability and made it difficult to determine dimensionality. *C,* However, the peak at high levels of predictability and $E = 4$ were restored when the 30-point time series from the other four species were combined with the 15 points used in *B.*

model has lagged linear residuals whose hidden functional form (quadratic) can be extracted using a residual-delay map (fig. B1; Sugihara et al. 1999). Finally, a simplex projection revealed that the five-species system was effectively four-dimensional (i.e., the next value in each series could be best predicted by the four preceding lagged values). Dissipative systems such as this, where a high-dimensional attractor is well modeled in lower dimensions, are mercifully common (see app. B). Using $E = 4$, we then constructed S-maps to perform pairwise predictions between species. In contrast to the AR model, the nonlinear cross-predictions had an error roughly one-quarter of the standard deviation (table B1; fig. 1C). Thus, in this model example, we see that apparently unrelated time series (statistically uncorrelated) can faithfully predict each other.

The high cross-predictability exhibited by this five-species model means that the species belong to the same dynamic equivalence class. That is, each species sees roughly the same attractor geometry. Insofar as each species' time series represents a similar shadow of the same object (attractor), superimposing these shadows on top of each other should reveal the attractor in greater detail, just as several sprinklings of dew progressively reveal more detail of a spiderweb. This increased resolution can be accomplished by "stitching" several time series together, end to end. Following convention, we suggest that data

for each time series be first-differenced and then normalized to unit mean and variance. The "seams" where two time series are stitched together are removed by discarding all embedding vectors that traverse a gap or seam. This long time series can then be used as the library set in the traditional methods above. We used the five-species model to demonstrate that the dimensionality, predictability, and nonlinearity apparent in a 1,000-point time series (figs. 2A, 3A) cannot be conclusively detected in a 30-point series (figs. 2B, 3B) but can be rescued by compositing the other four species (figs. 2C, 3C). The differences between the 1,000-point series and the composite series are negligible, despite a 97% reduction in data.

It is impossible to set a universal minimum on individual data series length. Among other factors, data requirements depend on the dimensionality of the underlying system (Ruelle 1989), the Lyapunov exponents, the sampling frequency, the noise in the system, observation error, and (as we suggest here) the number of equivalent series available for compositing. However, it is instructive to illustrate with our model example how power erodes as time series shorten. We progressively shortened our five-species time series and calculated the linear and nonlinear correlation and error for each of the five species as predicted by a composite of the other four. A weak nonlinear signal was detectable even with trivial samples (four ob-
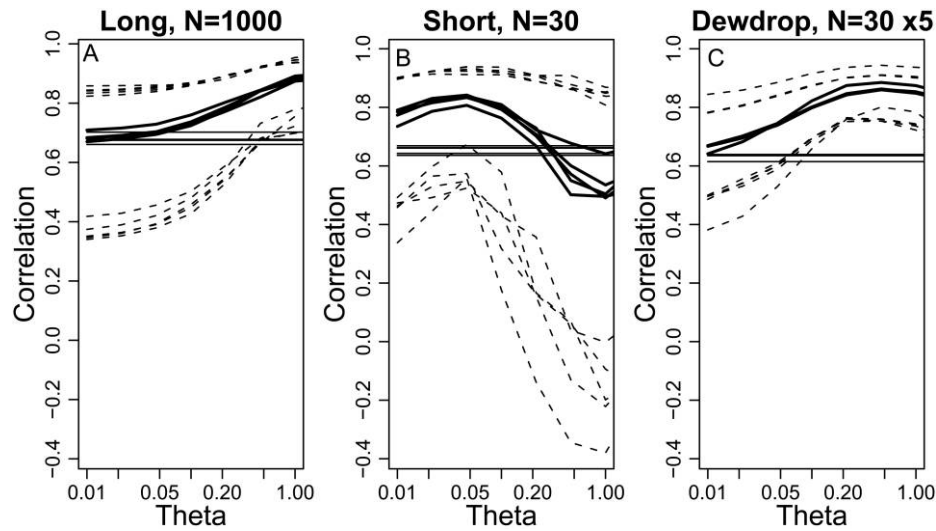
Figure 3: *A*, For each species in a five-species competition model, 15 points were forecast from a library of 985 (bootstrapped 1,000 times at 11 θ values for a total of 55,000 simulations). Linear correlation ($\theta = 0$; *thin lines*) was significantly worse than nonlinear correlation (*thick lines*; 95% confidence interval = *dashed lines*) at appropriate values of θ ($\theta = 0.5$ or higher). *B*, Forecasting 15 points with a library of just 15 was never statistically better than the linear model (close, but still NS at $\theta = 0.01$–0.05). *C*, However, nonlinearity and high levels of predictability were restored when the 30-point time series from the other four species were combined with the 15 points from *B* at $\theta = 0.5$.

servations), but statistical significance was lost at approximately 20 observations per series (fig. 4).

Although this procedure will generally be mathematically correct, caveat lector: the stitching of time series must be done with care. Specifically, it is important that compositing neither introduces nonlinearity when it is not there nor masks it when it is present. We suggest the following three tests to ensure accurate results.

Permutation Test

Because different permutations of time series give rise to different library and prediction sets, we suggest averaging over a large sample of time series combinations (connecting individual time series end to end in different orders to give different library/prediction sets). This permutation procedure is repeated 100 times or until all combinations are exhausted, and then the statistic of interest (e.g., correlation, error, θ) is computed as the average across all permutations. We use this procedure to confirm that linear processes remain linear after compositing ("AR + noise," table 1), as do nonlinear processes ("Logistic map" and "Five-species" models, table 1). This simple bootstrap procedure will reduce sampling error for the statistic of interest.

Homogeneous Set Test

Nonlinearity may appear as an artifact when linear time series that do not belong to the same equivalence class are stitched together ("Composite" section of table 1). A hypothetical example is demonstrated in figure 5*A*. Imagine 10 time series, where M1–M5 are generated from a linear-stochastic process (e.g., AR) and N1–N5 are generated by a different linear-stochastic process (e.g., noisy sine waves). If the library (L) and prediction (P) sets each contain time series from both M and N, then the composite series can show a spurious nonlinear signature. This happens because subset N4N5 is better forecast from a M1M2N1N2N3 composite library when the data of the similar time series N1N2N3 is more highly weighted in model construction and those of the subset M1M2 are down weighted. This differential weighting is how nonlinear forecasting operates. Thus, an artificial nonlinear signature might arise spuriously because of heterogeneity in the data.

This potential artifact can be eliminated if the library sets and prediction sets are constructed so that they are each maximally homogeneous (or if the library set is maximally different from the prediction set). If groups M and N are actually from the same equivalence class, artifacts will not appear. If groups M and N come from different processes, one should see no predictability when using M1–M5 as the library set and N1–N5 as the prediction set. Therefore, in addition to the permutation test, one should check whether nonlinearity is upheld when the
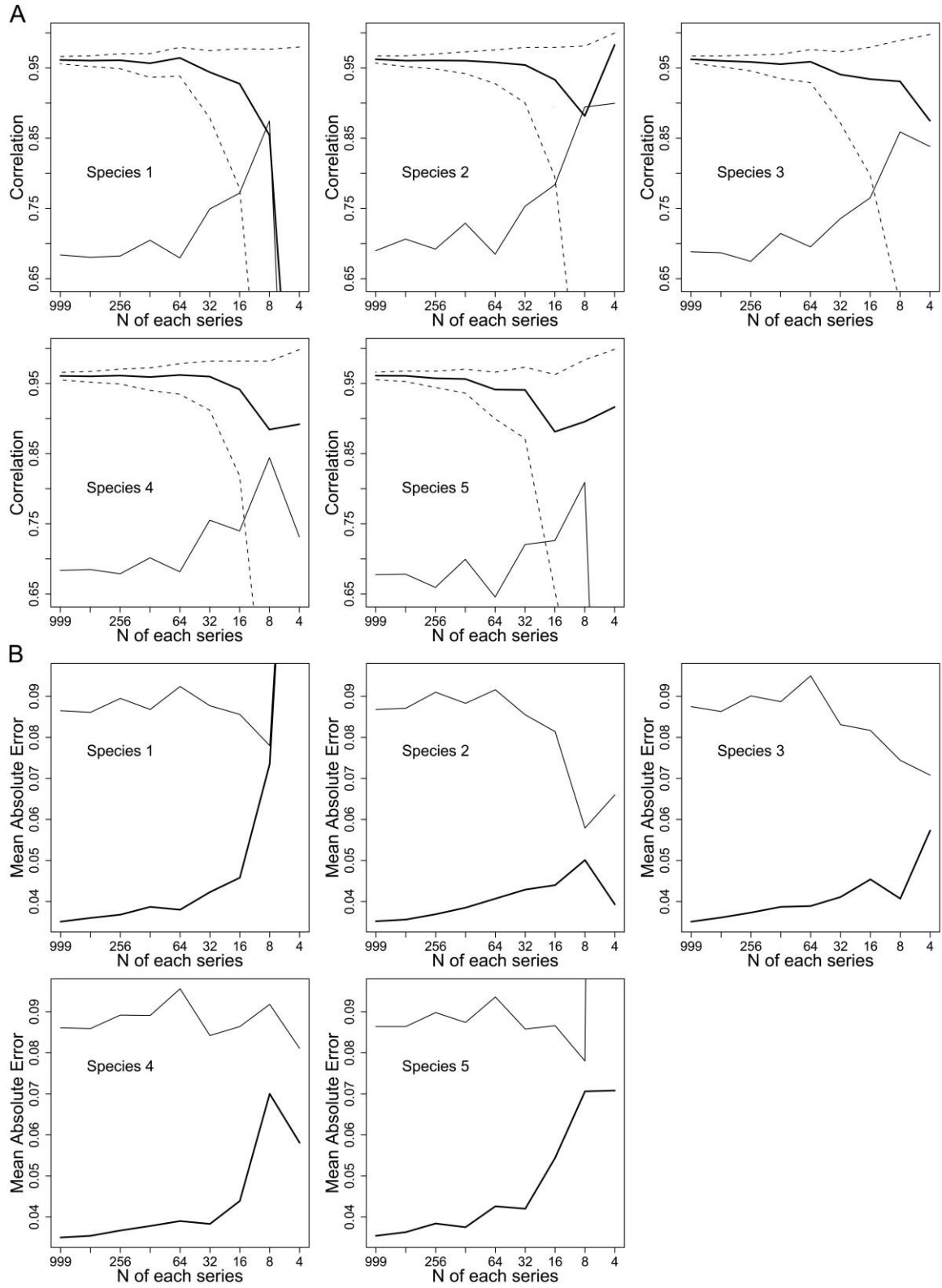
Figure 4: The decay of the nonlinear signal as time series length decreases, as measured by the decreasing correlation (*A*) and increasing mean absolute error (*B*). The thick lines represent a nonlinear model, the thin lines represent a linear model ($\theta = 0$), and the dashed lines represent a 95% confidence interval. Typically, significance was lost near $N = 20$, though a weak (nonsignificant) signal was detectable at even the smallest sample sizes.

Table 1: Results of the composite S-map

Data	Best E	Best θ (0 = linear)	Best ρ	$\Delta\rho$	Probability (Fisher)	Best MAE	ΔMAE	Probability (random)
Permutation test:								
AR + noise	10[a]	0	.330	0	1	.752	0	1
Logistic map	2	2	.888	.060*	<.01	.366	.081*	.01
Five-species model	4	6	.962	.273*	<.01	.035	.051*	.01
CalCOFI larval fish	5	.6	.603	.060*	.038	.577	.038*	.01
Composite of two linear processes produces a nonlinear artifact:								
AR + noise and sine waves	20[a]	2	.414	.07*	.032	.714	.021*	.01
Constructing homogeneous sets:								
AR + noise	10[a]	0	.325	0	1	.767	0	1
Logistic map	2	2	.889	.051*	<.01	.373	.068*	.01
AR + noise and sine waves	20[a]	0	−.094	0	1	1.188	0	1
CalCOFI costal fish larvae	5	.5	.666	.070*	.021	.582	.044*	.01
CalCOFI costal + oceanic	5	1.2	.587	.039	.313	.581	.022	.06

Note: AR + noise = 30 AR processes, $X_{t+1} = \alpha X_t + \varepsilon$, $\varepsilon \sim N[0, .5]$, $\alpha \sim U[0, 1]$, with 30 points for each time series. Logistic map = 30 series, $X_{t+1} = aX_t(1 - X_t) + b$, $a \sim U[3.6, 4]$, $b = 20\%$ error added after the simulation (Sugihara 1994). E = embedding dimension, θ = nonlinear tuning parameter, best ρ = forecast skill (correlation coefficient) using best θ (θ_{best}), $\Delta\rho = [(\rho$ at $\theta_{best}) - (\rho$ at $\theta_0)]$ and best mean absolute error (MAE) = forecast skill using best θ (θ_{best}), ΔMAE = (MAE at θ_0) − (MAE at θ_{best}). Thus, a positive $\Delta\rho$ or ΔMAE measures the difference in forecasting skill of the best nonlinear model (i.e., where $\theta > 0$) as compared to the global linear model (i.e., where $\theta = 0$). The significance of $\Delta\rho$ was tested by the Fisher's Z-test, and the significance of ΔMAE was tested by a randomization procedure.

[a] Maximum dimension testable.

* Significance at the .05 level.

library and prediction sets are selectively chosen to be maximally different (i.e., each set is internally homogeneous).

The following recipe can be used to construct groups with maximally homogeneous dynamics. First, using all of the time series together, find the order (ν) of the AR model with the best out-of-sample forecasting skill. Use a νth-order AR map (AR-ν) to perform pairwise prediction between each species' time series. This yields a linear (AR) predictability matrix (measured as correlation coefficients between predictions and observations). Note that this matrix is only roughly symmetrical; using series A to predict series B will be similar but not identical to using series B to predict series A. Next, use the predictability matrix to construct a similarity dendrogram based on linear copredictability. Here, we use $1 - r$ as a measure of distance and the unweighted pair group method with arithmetic mean to construct the dendrogram (Legendre and Legendre 1998). Last, use this dendrogram to determine groupings of species time series that give homogeneous library and prediction sets (fig. 5*B*). This procedure yields library sets of similar series that are most dissimilar to the prediction sets and will not produce artifacts of nonlinearity that might arise from pooling time series from unrelated dynamic processes. This should accompany the permutation test to double-check nonlinearity.

To illustrate this procedure, we simulate 15 time series from the AR process described in table 1 and 15 time series from noisy sine waves with random frequencies and phases. Each time series contains only 30 points. When the time series arising from the two kinds of dynamics appear in both the library and the prediction sets, we obtain an artificial nonlinear signature (table 1). Again, a false nonlinear signature appears because the composite is not homogeneous. To eliminate this source of artifact, we need to construct library and prediction sets so that each is dynamically homogeneous. We therefore construct the dendrogram of pairwise predictability for these series (fig. 5*B*). Based on this dendrogram, we use group I as the library set and group II as the prediction set. Not surprisingly, group I came from the AR process, and group II (and II′) were from noisy sine waves. Note that the remaining series have long branches, showing little pairwise predictability, and can be omitted to reduce uninformative noise in the analysis. The results, as expected, show low predictability and no improvement when the prediction is tuned toward nonlinear solutions (table 1). The results are the same when using group II as the library set and group I as the prediction set. Furthermore, this result (i.e., a linear signature with no nonlinear artifact) also applied to group II′, which was the same size as group I but was less homogeneous than either group I or II. Because nonlinearity vanished when time series were grouped, we concluded that groups I and II/II′ are not members of the same equivalence class and thus should not be combined into a composite.
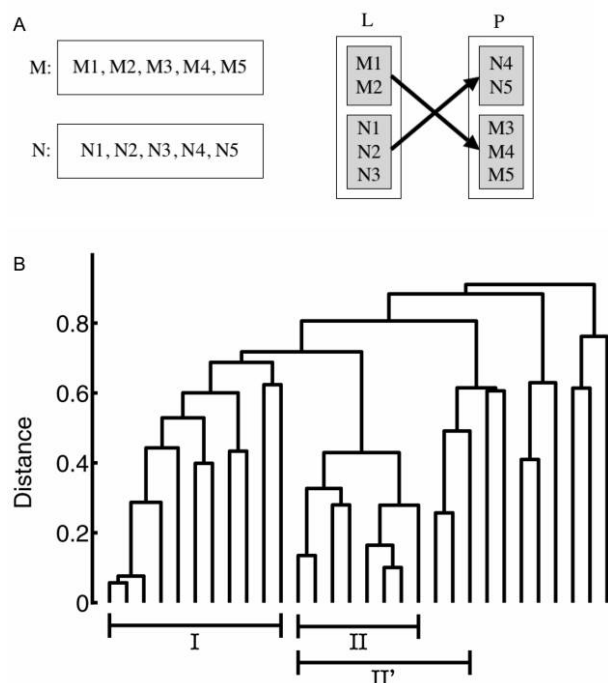
Figure 5: *A*, Schematic illustrating an artificial nonlinear signature generated when time series of different dynamic types are allocated into both the library (*L*) and the prediction sets (*P*). To avoid this statistical artifact, one needs to construct library and prediction sets that are each dynamically homogeneous. *B*, This can be achieved by constructing a similarity dendrogram based on pairwise predictions. According to the topology of the dendrogram, one should use set I to predict set II or II′, and vice versa. This procedure avoids an artificial nonlinear signature that can be generated from compositing heterogeneous sets.

Similar Shadow Test

Ecosystems contain many different populations that may not be ecologically similar. Processes in bacterial populations will have very different dynamics than the wolf populations in the same region, even if they have some influence on each other. As mentioned earlier, a technique for dealing with such data is presented elsewhere (C. N. K. Anderson, C.-h. Hsieh, and G. Sugihara, unpublished manuscript). Though analysis of ecologically heterogeneous time series is tractable with this second technique, dewdrop regression would probably have very little statistical power. How, then, can we objectively determine which to composite? A good way of ensuring that only dynamically similar species are grouped together is to directly test the similarity of their dynamics.

This test is similar to the homogeneous set test above but uses nonlinear forecasting in place of the linear AR model to define dynamic equivalence. Here the best order (embedding dimension) is determined with simplex pro-

jection, and pairwise correlations are determined using the S-map. Distant outgroups or deep branching might be regarded as evidence against including certain species in a composite. However, insofar as the ability to predict is the ultimate benchmark of success, a practical criterion for whether a time series should be included in the composite is whether it increases forecast skill.

Significance of Improvement of Nonlinear Forecast Skill

In the S-map procedure, nonlinearity is measured as a decrease in mean absolute forecast error (ΔMAE) or an increase in correlation ($\Delta\rho$) between predictions and observations. The key question is whether ΔMAE and $\Delta\rho$ are statistically significant. To test $\Delta\rho$, one can use Fisher's *Z*-test (Kleinbaum et al. 1998). To test ΔMAE, a simple bootstrap procedure can be used: (1) calculate ΔMAE from the composite S-map, denoted as statistic *T*; (2) randomly shuffle the data in the original time series and obtain a bootstrapped null ΔMAE, T^*; (3) repeat this procedure 100 times; (4) the ΔMAE is deemed significant if *T* is greater than 95 of the T^*s.

Applications in Real Data

We illustrate the overall approach with field data by applying dewdrop regression to larval abundances of coastal fish species collected in the California Cooperative Oceanic Fisheries Investigations (CalCOFI; Hsieh et al. 2005*a*). The CalCOFI data represent the longest oceanographic survey in the northeastern Pacific (from 1951 to 2002 with a gap between 1967 and 1983). Even in this long-term study, the time series of each individual species is barely sufficient to analyze at the annual scale. Therefore, we construct a composite time series for 23 coastal taxa, and we test it with dewdrop regression.

Because these coastal species live in the same area and presumably interact, it is not surprising to find that their time series of abundance can be treated as members of a dynamic equivalence class (table 1). In addition to the biological considerations, compositing these data is justified by the surprisingly high out-of-sample predictability obtained with the nonlinear forecast methods. Although the statistically significant gain in forecast skill achieved by including nonlinearity is modest in magnitude (0.603 vs. 0.543), the gains from compositing are truly dramatic; the S-map's forecast skill averaged 0.099 over the 23 individual time series, and the AR model of optimal order 5 averaged −0.045. If the coastal species do not belong to an equivalence class, we would not expect to see such high interannual predictability. More significantly, the permutation and homogeneous set tests indicate that the nonlinear signature is not a statistical artifact. Not surprisingly,

if data from other ecological domains (e.g., open ocean species) are included in the composites, the results deteriorate (table 1). We conclude that the dynamics of the CalCOFI coastal larval fishes can be well modeled by a low-dimensional attractor. The next step in modeling this system would be to search for physical or biological covariates that reduce dimensionality and increase forecast skill when included in the S-map analysis (for an example of this process, see Dixon et al. 1999).

The large gains in predictability achieved by compositing, linear or not, may be indicative of a significant phenomenon; any individual species time series becomes more predictable, given information about the other members of the community with which that species interacts. Indeed, the gains in predictability observed here are probably due to the clearer picture of the community dynamics provided by a 23-fold increase in sample size. The relatively weak nonlinear signal is a by-product of these data sets aggregating across slightly heterogeneous samples. There may be a trade-off in compositing depending on how heterogeneous the samples are; large heterogeneous sample sizes potentially can dampen the nonlinear signature. This effect has been seen in a variety of contexts (Sugihara 1994; Sugihara et al. 1996, 1999; Royer and Fromentin 2006) where aggregation tends to mask the nonlinear part of the signal. Because one might expect stronger nonlinear signatures on smaller scales (Sugihara et al. 1999; Hsieh et al. 2005*a*), any finding of nonlinearity in this context is therefore robust.

Conclusion

This article outlines techniques for extending nonlinear forecasting methods so that they can be applied to short ecological time series. These methods can be used to measure effective dimensionality and nonlinearity and improve forecasts in short ecological time series. Knowing how complex a system is—that is, the number of variables interacting, whether nonlinear interactions need to be emphasized, and how much predictability might be expected for the system—is an essential step to building better-informed models. Building a simple model for a system would be unrealistic if the data show that the number of free parameters required (dimensionality) for a given level of prediction accuracy is very large. On the other hand, if a system is found to be low dimensional, in principle, it should be feasible to develop a mechanistic forecast model to better understand how that system works (Dixon et al. 1999, 2001). For example, Dixon et al. (1999) identified the mechanisms explaining how three unrelated forcing mechanisms (lunar phase, turbulence, and wind direction) could cause episodic fluctuations in larval fish supply through their nonlinear "perfect-storm-like" combination. This gives rise to a multivariate form of phase-space reconstruction (embedding) where the coordinate axes were explicitly the three physical variables in operation (lunar phase, turbulence, and wind direction). This example demonstrates that even with lagged-coordinate constructions of just one time series, nonlinear methods can exhibit powerful forecasting ability and can represent a clear step toward better prediction and understanding of natural systems.

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