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Quantifying temporal change in biodiversity: challenges and opportunities

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Proc. R. Soc. B published online 24 October 2012
doi: 10.1098/rspb.2012.1931

Supplementary data
"Data Supplement"
http://rspb.royalsocietypublishing.org/content/suppl/2012/10/18/rspb.2012.1931.DC1.html

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Review

Quantifying temporal change in biodiversity: challenges and opportunities

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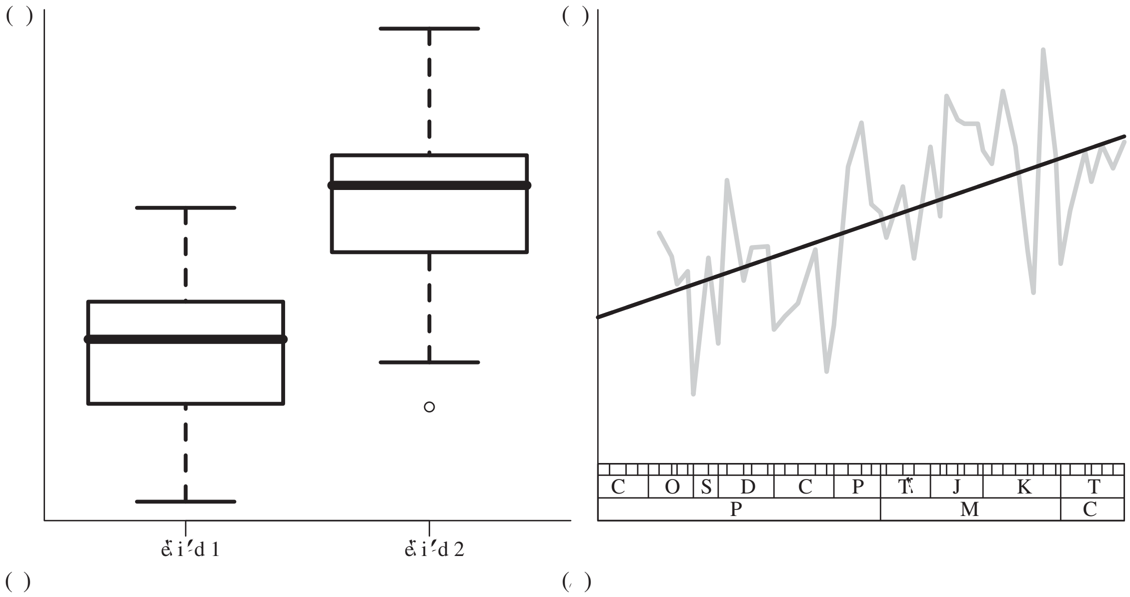
biodiversity, ecosystem services and hypothesized driver variables are among the strongest possible evidence for causal links. Moreover, temporal studies of biodiversity are essential for forecasting future change in community structure and ecosystem function.

We begin by discussing key characteristics of biodiversity time series, presenting details on the advantages and limitations of different data sources in the electronic supplementary material. Second, we address the quantitative analysis of biodiversity time series, identifying four main factors affecting observed biodiversity temporal change: measurement error, process error, systemic change and historical influence. We discuss methods used to estimate, quantify or (when appropriate) minimize these sources of change. Third, we highlight approaches and potential pitfalls in forecasting biodiversity change, on the basis of inferences drawn from past trends. We are restricted to time series of one (any) quantitative metric of biodiversity. We are purposely agnostic about which metric, and illustrate that the same analysis tools can be used for different metrics. We highlight that anecdotal evidence and historical records can provide important information, which need only be translated into a quantitative assessment for these tools to be useful for this sort of data.

2. CHARACTERISTICS OF TEMPORAL BIODIVERSITY DATA

A biodiversity time series documents the abundances (or at least presence–absence) of multiple genes, traits or taxa at multiple points in time. Taxa—species, in particular—are the most common units of diversity, but most of the methods we discuss are also applicable to other units of diversity (see figure 1 and electronic supplementary material, figures S4 and S5 for an illustration of this point). These data are typically used to estimate one or more biodiversity metrics at each time point. Common diversity metrics include species richness (the total number of spe



temporal resolution. Increased census interval tends to be associated with increased temporal turnover [21,22].

3. ANALYSING TEMPORAL CHANGE

Regardless of the methods used to gather data (see the electronic supplementary material), observed temporal change in biodiversity can be attributed to four main factors: measurement error, process error, historical influence and systemic change. Measurement error includes sources of apparent change that reflect bias or imprecision in measurement (including detection error), and can reduce our ability to identify patterns of interest. Process error refers to mechanisms that are not included in the model, and is different from measurement error. Historical influence is reflected in the patterns of temporal autocorrelation of the biodiversity time series. Typically, we are interested in understanding the effects of particular drivers of interest on systemic change. Systemic change reflects a non-stationary system in which there are long-term changes in ecological drivers, both anthropogenic (ongoing climate change and increases in nutrient deposition) and natural (shorter-term successional change and long-term changes in speciation and extinction rates). Temporal change due to other drivers may occur as a result of process error, and this partitioning depends on the questions being addressed. Explicitly recognizing sources of error allows the investigator to statistically control for these when testing for systemic change in a biodiversity time series (see the electronic supplementary material, figure S1 for an particularly informative in assessing causality because the timing of events makes it possible to deduce the direction in which information is being transferred [48]. Both temporal and spatial data are affected by autocorrelation, with points closer in space or time on average more similar than distant points. As a result, at least in realistic ecological situations, variability typically increases with increasing extent [49]. However, the nature of autocorrelation differs between time and space in three subtle ways. First, a focal point in space can influence and be influenced by nearby points in three dimensions, whereas a focal point in time can be influenced only by points that precede it and can only influence points that follow it chronologically. This does not necessarily mean that spatial autocorrelation is stronger, because effects on a focal point from different directions can be counteracting. Because of the three dimensions, there is also the possibility of anisotropy (different covariances in different directions) in space but not in time. Second, the underlying autocorrelation in time, arising at least in part because some or all organisms survive into the next time period, is generally intrinsically stronger than any type of spatial influence, where the most direct causal factor is dispersal or environmental autocorrelation. Third, from an empirical point of view, cycles are common and important in temporal but rare in spatial autocorrelation patterns.

In practice, the study of autocorrelation in space and time typically differs in three ways. First, temporal data are typically collected at constant time intervals, allowing easy calculation of lags between points, whereas spatial variables are often recorded at irregular locations distributed continuously in space, requiring the use of techniques such as binning distances to estimate variograms. Second, for historical reasons, variograms (based on variance) are typically used for spatial autocorrelation, while correlograms or autocorrelation function)12.6(n)-394.8()12.6(n)-39477(i

regression. Among many statistical models, generalized additive models (GAMs) [66] are widely used to fit smooth curves or surfaces to data over time for this purpose. GAMs extend generalized linear models and assume additive relationships among the effects of predictors, allowing data to determine the (generally nonlinear) relationship between the response variable and the set of predictors (see electronic supplementary material for more detail and extension into the spatio-temporal case).

A common method for short-term trend models is to use cubic regression splines to construct each smooth function, applying the penalized regression spline technique [67], which controls the degree of smoothness by adding a penalty to the likelihood function. This model usually provides a better fit than parametric linear or quadratic models. Many other smoothing methods are available, including piecewise regression, kernel methods, LOESS (locally weighted polynomial regression), running-mean (or running-median) smoothers, classification and regression tree, and multivariate adaptive regression splines [66,68]. Figure 1c shows two local models (LOESS and GAM with splines) fitted to the fossil shell size diversity time series. A comparison with figure 1b illustrates the complementary nature of global and local models: despite a long-term increase in diversity of this trait, the rate of change has not been constant.

Non-parametric smooth functions are not only suffipressures upon ecosystems, generating novel systems [80] that function differently, as the pool of functional traits changes [81], and combinations of environmental variables arise that have no contemporary analogues [82]. In many cases, palaeo-climates encompass a greater range of projected conditions and may provide important clues for expected biotic responses [83]. These issues create challenges for predicting biodiversity trends that require us to understand the mechanisms driving diversity and call for placing greater statistical weight on datasets that better represent the anticipated change.

5. CONCLUSIONS

Availability of long-term, large-scale, high-resolution data is the single most important factor limiting progress in understanding temporal patterns in biodiversity. Given the difficulty of obtaining data from the past, we reiterate the appeal to preserve data and associated metadata in publicly accessible archives [84]. Public databases of biodiversity records are providing unprecedented insight into large-scale, long-term patterns (e.g. Paleobiology database—http://paleodb.org, Global Biodiversity Information Facility—http://data.gbif.org/). Establishing standards for meta-information should ensure that future scientists can not only access but also take full advantage of the data we are now collecting [85]. The challenges that arise from dealing with historical data (see the electronic supplementary material) should help sih9(iok7ng)-354l..5(r)307.8(dai4k7ng)-35t(ec)17((to)]T[3.49as)-182(ta)18.3(3313.2(th)ts)15.26(l-i31.4(er(le

19 Behrensmeyer, A. K., Kidwell, S. M. & Gastaldo, R. A. 2000 Taphonomy and paleobiology. In *Deep time: paleobiology's perspective* (eds D. H. Erwin & S. L. Wing), pp. 103–147. Boulder, CO: Paleontological Society.

20 Alroy, J. 1996 Constant extinction, constrained diversification, and uncoordinated stasis in North American mammals. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **127**, 285–311. (doi:10.1016/S0031-0182(96)00100-9)

21 Diamond, J. M. & May, R. M. 1977 Species turnover rates on islands: dependence on census intervals. *Science* **197**, 266–270. (doi:10.1126/science.197.4300.266)

22 Russell, G. J., Diamond, J. M., Pimm, S. L. & Reed, T. M. 1995 A century of turnover: community dynamics at three timescales. *J. Anim. Ecol.* **64**, 628–641. (

59 Cuddington, K. M. & Yodzis, P. 1999 Black noise and population persistence. *Proc. R. Soc. Lond. B* **266**, 969–973. (doi:10.1098/rspb.1999.0731)

60 Hallett, T. B., Coulson, T., Pilkington, J. G., Clutton-Brock, T. H., Pemberton, J. M. & Grenfell, B. T. 2004 Why large-scale climate indices seem to predict ecological processes better than local weather. *Nature* **430**, 71–75. (doi:10.1038/nature02708)

61 Gumpertz, L. & Pye, M. 2000 Logistic regression for southern pine beetle outbreaks with spatial and temporal autocorrelation. *Forest Sci.* **46**, 95–107.

62 Buckland, S. T., Magurran, A. E., Green, R. E. & Fewster, R. M. 2005 Monitoring change in biodiversity through composite indices. *Phil. Trans. R. Soc. B* **360**, 243–254. (doi:10.1098/rstb.2004.1589)

63 Connolly, S. R., Dornelas, M., Bellwood, D. R. & Hughes, T. P. 2009 Testing species abundance models: a new bootstrap approach applied to Indo-Pacific coral reefs. *Ecology* **90**, 3138–3149. (doi:10.1890/08-1832.1)

64 Buckland, S. T., Cattanach, K. L. & Anganuzzi, A. A. 1992 Estimating trends in abundance of dolphins associated with tuna in the eastern tropical Pacific Ocean, using sightings data collected on commercial tuna vessels. *Fishery Bull.* **90**, 1–12.

65 Schenker, N. & Gentleman, J. F. 2001 On judging the significance of differences by examining the overlap between confidence intervals. *Am. Stat.* **55**, 182–186. (doi:10.1198/000313001317097960)

66 Hastie, T. J. & Tibshirani, R. J. 1990 *Generalized additive models*. London, UK: Chapam and Hall/CRC Press.

67 Ruppert, D., Wand, M. P. & Carroll, R. J. 2006 *Semi-parametric regression*. New York, NY: Cambridge University Press.

68 Leathwick, J. R., Elith, J. & Hastie, T. J. 2006 Comparative performance of generalized additive models and multivariate adaptive regression splines for statistical modelling of species distribution. *Ecol. Model.*

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