



Detecting temporal trends in species assemblages with bootstrapping procedures and hierarchical models

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imperfect detection. Instead, most methods assume that the absence of a species from a sampling period represents a 'true' zero, and not a detection error (Royle & Dorazio 2008). Most procedures also ignore species that may have been present in a region, but were never detected in any of the samples (Colwell & Coddington 1994).

In this study, we develop new methods for quantifying temporal trends in species abundances that account for errors in detection of individuals. Our methods are appropriate for analysing species-specific

were true by comparing the observed TC to the histogram of simulated TC values.

Because the results are potentially sensitive to the assumption of simple linear trends in $\log_{10}(\text{TC})$, we fit two alternative regression models based on log-log and log-linear transformations of $(\text{TC} + 1)$ and $\log_{10}(\text{TC})$. The same transformations were applied to the real and the simulated data. Although these alternative models incorporated nonlinear trends in species temporal trajectories, the transformations had no qualitative effect on the outcome of the null model tests. Therefore, we present results only from analyses of the untransformed data fit with a linear trend line.

(c) Undetected species

The construction of the null matrix is similar to a simulation of rarefaction (Sanders 1968; Hurlbert 1971), in which a small assemblage is simulated by random draws of subsamples of n individuals from the larger sample of N . However, in rarefaction, sampling is done without replacement (Simberloff 1978). Because our null model treats the source pool as a permanent stationary distribution, we sampled from it with replacement. In practice, the results will not differ unless the sample sizes are so small that n is a relatively large fraction of N , which is not the case for these datasets. Rarefaction also conditions on n , the observed count in a particular sample, whereas our multinomial model conditions on N , the total number of individuals.

This procedure implicitly addresses detection error because species (especially rare ones) that are present in the aggregated collection N may not be represented in any particular sample n . In some null assemblages, species that were very rare in the original dataset may be missing from all n samples. Because biodiversity sampling is notoriously incomplete, there are also likely to be rare species in the assemblage that were never encountered in the original samples (Colwell & Coddington 1994). We expanded our null model to incorporate these undetected species. We first estimated the minimum number of undetected species, \hat{S}_{min} , using a bias-corrected version of the familiar Chao2 estimator (Chao 1984; eqn (2.4) in Colwell 2009)

$$\hat{S}_{\text{min}} = \left(\frac{S_1 - 1}{S_2} \right) \left(\frac{S_1(S_1 - 1)}{2(S_2 + 1)} \right), \quad (2.11)$$

where S_1 is the number of species represented in exactly 1 time period ('uniques'), S_2 is the number of species represented in exactly two time periods ('duplicates') and S is the number of samples. The Chao2 index estimates the number of undetected species in the entire assemblage, not the number that may be undetected in any single sample. For the stream fish matrix, the estimated number of undetected species (rounded to the nearest whole integer) was 16. For the insect matrix, sampling was restricted to nine common species, and the estimated number of undetected species was 0.

Once the number of undetected species was estimated, it was necessary to assign them each a relative abundance p_i , so they could be included in

the simulation. Estimating these p_i values would require knowledge of the precise form of the species abundance distribution, a long-standing unsolved problem in ecology (McGill *et al.* 2007). As a simplifying first approximation, we assumed that p_i for each undetected species was equal to 0.5; for the least abundant species observed in the assemblage. The reasoning is that if any of these undetected species occurred at a frequency greater than this, they would probably have been detected at least once in the original sample. For the stream fish data, p_i for each of the 16 undetected species was set at 3.414135×10^{-5} . Because many of the undetected species are probably much more rare than this, our procedure allows for the greatest possible influence of undetected species. Nevertheless, the results for the stream fish matrix were identical with and without the inclusion of undetected species. However, because the observed number of species is always a biased under-estimator of true species richness, we present the full analyses here with the undetected species included in the null model.

If the observed value of TC is larger than those of 950 of the 1000 simulated TC values ($\zeta < 0.05$, one-tailed test), then the temporal trends in the set of observed species are more heterogeneous than can be accounted for by the null model: at least some species are either increasing or decreasing more rapidly than would be expected from sampling effects and undetected species. The null model was programmed and implemented in the statistical language R (R Development Core Team 2008; see electronic supplementary material, appendix A).

(d) Hierarchical model of trend in abundances

The null model provides a simple test for

of N , with the level of bias depending on the magnitude of p , the unknown probability of capture for individuals of species i .

In the absence of replicated observations, we cannot estimate temporal changes in both N and p . Therefore, we assume that capture probabilities vary among species but not among surveys (i.e. we assume $p_{i,t} = p_i$). Even with this simplifying assumption, the hierarchical model composed of equations (2.12)–(2.14) contains more parameters than can be estimated from the data. To solve this problem, N may be eliminated from the model by integrating the joint distribution of p and N . This integration can be done analytically to obtain the following marginalized version of the hierarchical model:

$$y_{i,t} | \lambda_0, r_i \sim \text{Poisson}(\lambda_0 \exp(r_i t)). \quad (2.15)$$

Note that this model may be viewed conceptually as a Poisson regression model. For example, let μ denote the Poisson mean for $y_{i,t}$. The logarithm of μ is a linear combination of the marginal model's parameters

$$\log(\mu_{i,t}) = \log(\lambda_0) + r_i t. \quad (2.16)$$

However, λ_0 and r_i are not identifiable parameters in equation (2.16) (i.e. both parameters cannot be estimated); therefore, we combine these parameters into a common regression intercept parameter (say, $\mu = \log(\lambda_0)$) to obtain

$$\log(\mu_{i,t}) = \mu + r_i t. \quad (2.17)$$

From this equation, the observations, $y_{i,1}, y_{i,2}, \dots, y_{i,T}$, can be used to estimate the parameters μ and r_i . We are interested primarily in the latter parameter r_i , which denotes the trend in abundance of species i ; however, our formulation of the intercept parameter μ reveals explicitly the combined roles of mean abundance and capture probability in the model.

The model specified by equations (2.15) and (2.17) can be fitted to each species separately. However, doing so may produce estimates of trend that are unstable or highly imprecise for species whose abundance appears to be low (as indicated by counts that contain several zeros and ones). Therefore, we extend the model as follows:

$$r_i | \beta, \sigma \sim \text{normal}(\beta, \sigma^2) \quad (2.18)$$

where β denotes the average trend in abundance among species in this assemblage and σ denotes the level of variation in r_i values among species. This distributional assumption allows the counts of all species to be analysed jointly so that information associated with species of moderate or high abundance can be used to stabilize the estimates of trend for species of low apparent abundance. Nevertheless, even with this assumption, there were not enough data to reliably estimate trends for very rare species that were represented by less than 10 individuals in the entire survey (25 of 55 stream fish species, and two of nine insect species).

Equation (2.18) implies an exchangeability of trend parameters among species. This exchangeability formalizes the notion that although abundances may be

increasing, decreasing or constant for any particular species, each is also a member of a common assemblage. We expect that the temporal trends of the species in the stream fish assemblage are more similar to one another than they are to, say, the temporal trends of the species in the grassland insect assemblage. A restricted version of this model that corresponds to the null model assumes an identical growth rate $r_i = \beta$ for all species, so that $\sigma = 0$. We can fit this restricted model and compare it with the unrestricted model to assess whether the data support the null hypothesis that all species abundances have an identical trend.

(e) Method of estimation

The hierarchical model described by equations (2.15), (2.16) and (2.18) may be fitted by maximizing the likelihood function obtained by integrating away the latent trend parameters. In our situation, however, this approach is counter-productive. In addition to the minor technical challenges of computing the integrals numerically, the trend parameters r_i are the quantities of primary scientific interest. Estimates of these parameters and their uncertainties are actually needed to solve the inference problem. We therefore adopt a Bayesian approach to inference, which allows every parameter in the model to be estimated directly, including the species-specific trends in abundance.

In a Bayesian analysis, all inferences are based on the joint posterior distribution of model parameters. In our case the unnormalized, probability density function (pdf) of this distribution is

$$\begin{aligned} \pi(\mathbf{a}, \mathbf{r}, \beta, \sigma | \mathbf{Y}) &\propto \pi(\beta, \sigma, \mathbf{a}) \prod_{i=1}^S g(r_i | \beta, \sigma) \\ &\times \prod_{i=1}^S (\cdot | \mu_{i,t} \exp(\mu + r_i t)), \end{aligned} \quad (2.19)$$

where $\mathbf{a} = (a_1, \dots, a_S)'$, $\mathbf{r} = (r_1, \dots, r_S)'$, and $\mathbf{Y} = (y_1, \dots, y_S)'$. Here, $g(\cdot | \beta, \sigma)$ denotes the pdf of a normal distribution with mean β and variance σ^2 , $(\cdot | \mu)$ denotes the probability mass function of a Poisson distribution with mean μ , and $\pi(\beta, \sigma, \mathbf{a})$ denotes the pdf of the prior distribution of the parameters β , σ , and \mathbf{a} .

The posterior pdf cannot be written in closed form owing to the analytically intractable integrals in the normalizing constant (not shown in equation (2.19)). Therefore, we estimated the model's parameters using Markov chain Monte Carlo algorithms (Robert & Casella 2004) to obtain an arbitrarily large sample of the joint posterior distribution. Specifically, we fit the model using the WinBUGS software (Lunn *et al.* 2000), which is an implem022500sc200210T05.t16.2ltes the

'burn-in', and every fifth draw in the rest of each chain was retained to form the posterior sample. Consequently, these calculations yielded a posterior sample of 20 000 draws, which was used to compute estimates of the model's parameters and their 95% credible intervals (see electronic supplementary material, appendix B).

3. RESULTS

(a) Null model analysis

For the stream fish data, there was a non-significant decreasing trend in total abundance (figure 1), caused primarily by extremely high abundances in the November 1966 sample ($n = 5344$ individuals). For the null model analysis, this decreasing trend leads to the expectation of negative slopes for individual species, with a moderate amount of variation among species (figure 2). However, the observed slopes were much more heterogeneous than this expectation: several species showed sharply increasing or decreasing trend lines (figure 2), and the observed TC index was larger than that of all 1000 simulated assemblages (table 1).

For the insect data, there was a marginally non-significant increasing trend in total abundance (figure 3), with systematically greater abundances during the final sampling years. For the null assemblages created from this matrix, most species had increasing trend lines (figure 4). However, the observed slopes were again much more heterogeneous than expected (figure 4). As with the stream fish data, the observed heterogeneity among slopes (TC) was greater than that of any of the simulated assemblages (table 1).

(b) Trends in abundances

For the stream fish data, the hierarchical model identified seven species with significant increases in abundance, 17 species with significant declines in abundance and six species with no significant trend (figure 5). A negative estimate of average trend, $\hat{\beta} = -0.152$ (95% credible interval: $(-0.289, -0.024)$), also indicates that species with declining abundances outnumbered those with increasing abundances. There is little doubt that trends in population abundance differed substantially among species. The posterior distribution of σ (figure 6) provides virtually no support for the hypothesis that $\sigma = 0$.

For the grassland insect data, the hierarchical model identified two species with significant increases in abundance, three with significant declines in abundance and 15 species with no significant trend (figure 5). A positive estimate of average trend, $\hat{\beta} = 0.152$ (95% credible interval: $(0.024, 0.289)$), also indicates that species with increasing abundances outnumbered those with declining abundances. There is little doubt that trends in population abundance differed substantially among species. The posterior distribution of σ (figure 6) provides virtually no support for the hypothesis that $\sigma = 0$.

abundance405469(six)-467.93.2(cies)-40.8(ewith)9.16(with)-878.4(signific.9311.8(nt)-467(trend)]TJT*(0)Tj0.0705900.3058

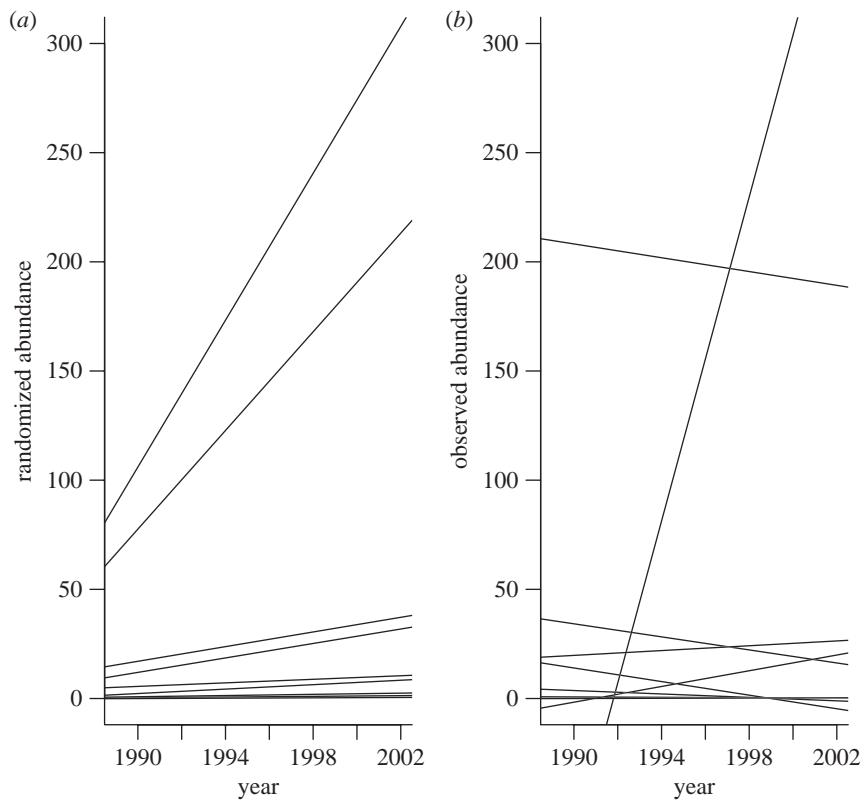
(Grossman & Sabo 2010). The decreasing trends in abundance of many stream fish species (figure 5) are consistent with a shifting baseline scenario, but the causes of these declines are still unknown.

The results of both the null model and the hierarchical model are potentially sensitive to the functional form that is used to describe temporal trends. For the null model analysis, the results for these datasets were the same when the trends were fit with linear,

semi-logarithmic, or log-log transformations of the original data. The estimated heterogeneity among species in temporal trends does not seem to be sensitive to the fitting procedure, perhaps because deviations caused by extreme sample numbers (such as the high counts in the stream fish dataset in 1966) are also incorporated into the pattern in the null assemblages. Both the null model and the hierarchical model assume that species are independent of one another. However, it is unclear how the violation of this assumption (from strong species interactions) would systematically affect the estimates of temporal trends in abundance.

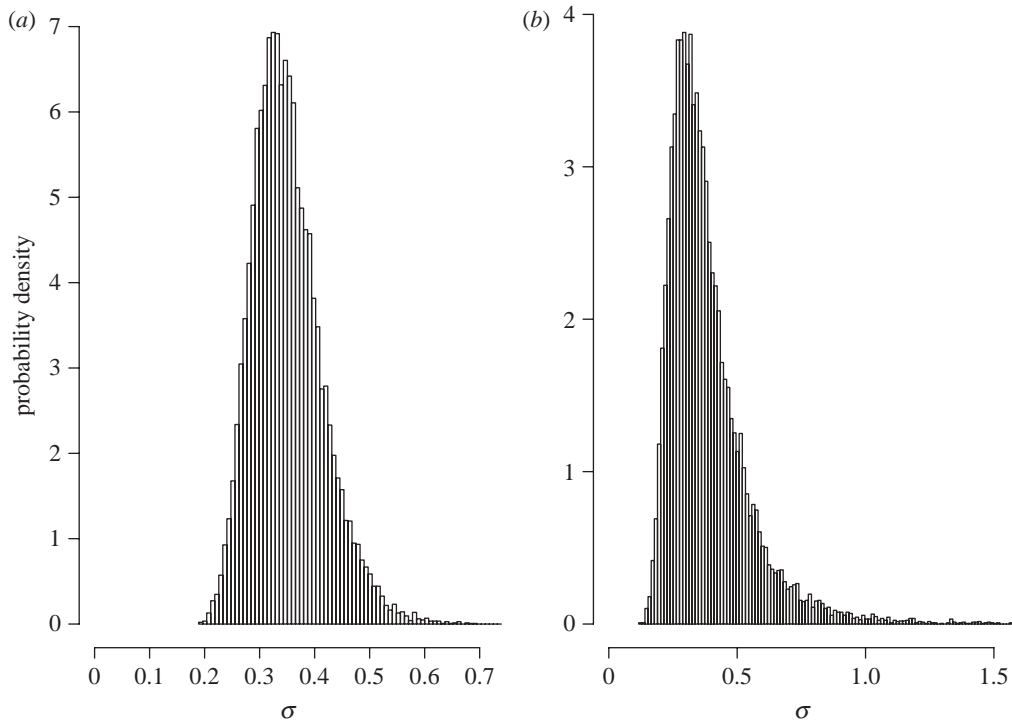
Because the hierarchical model is being used for parameter estimates of change (rather than just a simple dichotomous null model test), it is potentially more sensitive to violation of its assumptions. As we noted, one important assumption in this model is that capture probabilities are constant through time. Although this assumption may not be true, it probably matches the perspective of most field biologists, who typically assume that long-term monotonic changes in species counts with standardized sampling methods primarily reflect changes in abundance, rather than changes in detection or capture probabilities.

If species-specific capture probabilities are not constant, the magnitude of the deviations between observed and expected counts may be inflated. As long as these deviations do not vary systematically with time, the point estimates of trend will not be affected, although the credible intervals may be too narrow. Alternatively, if the deviations between expected and observed counts vary systematically with time, the point estimates of trend will be affected. As



with time, say changing from positive to negative values, the trend estimates will be very sensitive to an incorrect assumption of constant capture probability. For the datasets we analysed, there was no evidence of a systematic lack of fit (figure 8).

In the hierarchical model, the assumption of constant sampling probabilities was necessary only because of the extremely simple and unreplicated structure of the data matrix. With replication, it may be possible to estimate parameters for temporal



trends in both abundance and detection probabilities. For example, the KBS insect data actually consist of weekly sticky trap counts collected from six replicated plots. Rather than pooling the data as we have done in this analysis, the individual trap records could be fit to a more complex hierarchical model (Royle & Dorazio 2008; Kéry *et al.* 2009). The hierarchical model could also be expanded to incorporate species-specific covariates \mathbf{Z} (such as body size, geographical range size, or degree of habitat specialization) that might be of interest for conservation purposes. Species-specific covariates could be used to model either the mean structure of the elements of \mathbf{r} in equation (2.18) or their covariances.

Both the bootstrap test and the hierarchical model assume that changes in abundance through time are monotonic. If species show more complex patterns of temporal change (such as periodic fluctuations), these could be accommodated by fitting polynomial or sine functions to the time series. However, at least for these datasets, diagnostic analysis of residuals indicated little evidence for departures from linearity over the time periods that were sampled. Moreover, a monotonic function is appropriate for very short data series such as these ($n = 15$ samples for stream fishes and $n = 14$ samples for grassland insects).

Finally, the frequent occurrence of rare species in natural assemblages continues to pose statistical

- Colwell, R. K. 2009 *Ecol. Modelling*, v. 8.2. User's Guide and application published at: <http://purl.oclc.org/estimates>.
- Colwell, R. K. & Coddington, J. A. 1994 Estimating terrestrial biodiversity through extrapolation. *Conserv. Biol.* **345**, 101–118. (doi:10.1098/rstb.1994.0091)
- Connell, J. H. & Slatyer, R. O. 1977 Mechanisms of succession in natural communities and their role in community stability and organization. *Amer. Nat.* **111**, 1119–1144.
- Dixon, P. M., Ellison, A. M. & Gotelli, N. J. 2005 Improving the precision of estimates of the frequency of rare events. *Ecol. Modelling* **86**, 1114–1123. (doi:10.1890/04-0601)
- Dorazio, R. M., Kery, M., Royle, J. A. & Plattner, M. 2010 Models for inference in dynamic metacommunity systems. *Ecol. Modelling* **91**, 2466–2475. (doi:10.1890/09-1033.1)
- Dunson, W. A. & Travis, J. 1991 The role of abiotic factors in community organization. *Amer. Nat.* **138**, 1067–1091.
- Ellison, A. M. 2005 Loss of foundation species: consequences for the structure and dynamics of forested ecosystems. *Forest Ecology and Management* **3**, 479–486. (doi:10.1890/1540-9295(2005)003[0479:LOFSCF]2.0.CO;2)
- Fujiwara, M. & Mohr, M. S. 2009 Identifying environmental signals from population abundance data using multivariate time-series analysis. *Oecologia* **118**, 1712–1720. (doi:10.1111/j.1600-0706.2009.17570.x)
- Gilks, W. R., Thomas, A. & Spiegelhalter, D. J. 1994 A language and program for complex Bayesian modelling. *Comput. Stat.* **43**, 169–178. (doi:10.2307/2348941)
- Gotelli, N. J. & Colwell, R. K. 2001 Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecol. Letters* **4**, 379–391. (doi:10.1046/j.1461-0248.2001.00230.x)
- Gotelli, N. J. & Graves, G. R. 1996 *Null Models in Ecology*. Washington, DC: Smithsonian Institution Press.
- Grossman, G. D. & Sabo, J. L. 2010 Incorporating environmental variation into models of community stability: examples from stream fish assemblages. In *Community Ecology* (eds K. Gido & D. Jackson), Washington, DC: American Fisheries Society.
- Grossman, G. D., Moyle, P. B. & Whittaker Jr, J. O. 1982 Stochasticity in structural and functional characteristics of an Indiana stream fish assemblage: a test of community theory. *Amer. Nat.* **120**, 423–454.
- Grossman, G. D., Freeman, M. C., Moyle, P. B. & Whittaker Jr, J. O. 1985 Stochasticity and assemblage organization in an Indiana stream fish assemblage. *Amer. Nat.* **126**, 275–285.
- Grossman, G. D., Ratajczak, R. E., Crawford, M. K. & Freeman, M. C. 1998 Assemblage organization in stream fishes: effects of environmental variation and interspecific interactions. *Ecology* **68**, 395–420. (doi:10.1890/0012-9615(1998)068[0395:AOISFE]2.0.CO;2)
- Hurlbert, S. H. 1971 The nonconcept of species diversity: a critique and alternative parameters. *Ecol. Modelling* **52**, 577–585. (doi:10.2307/1934145)
- Jones, C. G., Lawton, J. H. & Shachak, M. 1994 Organisms as ecosystem engineers. *Oecologia* **69**, 373–386. (doi:10.2307/3545850)
- Kellogg Biological Station Sampling Protocols 1995 See <http://lter.kbs.msu.edu/protocols/36>.