Estimating Species Richness

Kevin M. Clarke
Fall 2005 - Annotated Bibliography

Colwell, R. K., and Coddington, J. A. 1994. **Estimating terrestrial biodiversity through extrapolation.** *Philosophical Transactions of the Royal Society (Series B)* **345**:101-118.
One of the broadest overviews (and most cited) of species estimation by extrapolation. This should be read first.
RATING: 5

Longino, J., Coddington, J. A., and Colwell, R. K. 2002. **The ant fauna of a tropical rainforest: estimating species richness three different ways.** *Ecology* **83**:689-702.
An excellent study testing all species richness estimation methods. This paper should be read second.
RATING: 5

O'Hara, R.B., 2005. **Species richness estimates: How many species can dance on the head of a pin?** *J. Anim. Ecol.,* **74**: 375-386.
Very good paper giving a summary and comparison of several species richness estimators. O'Hara looked at two non-parametric (ACE and Chao1), four based on rarefaction curves (Michaelis-Menton and exponential curve) and two by fitting abundance distributions (poisson and gamma distribution). The paper concludes that it is difficult to estimate species richness because the only way to know you are getting true species richness is to know the abundance distributions, which is often impossible, and knowing their catchabilities. Therefore, bias can't be estimated. Non-parametric estimates only give lower bound estimates and should be used with caution.
RATING: 5

Gotelli, N. J., and R. K. Colwell. 2001. **Quantifying biodiversity: Procedures and pitfalls in the measurement and comparison of species richness.** *Ecology Letters* **4**:379-391.
Good paper on comparing a sample based vs. individual based to sampling.
This paper highlights the distinction between individual-based assessment protocols, where individuals are sampled sequentially, and sample-based assessment protocols, in which sampling units, such as quadrats, are identified, and all the individuals that lie within them are enumerated. In many studies these data sets are often treated as interchangeable and this paper points out that they shouldn't because it can lead to different conclusions about species richness. An example given is when the same assemblage is analyzed using both methods, sample-based species accumulation curves typically lie below individual-based curves. This happens because environmental heterogeneity leads to non-random distribution of species amoung samples.
RATING: 4

Soberón, M. J., and B. J. Lorente. 1993. **The use of species accumulation functions for the prediction of species richness.** *Conservation Biology* **7**:480–488.
A highly cited paper that is a broad overview of species accumulation functions. It examines three different models (Clench, Exponential, and Logarithmic) in great depth and explains which model is best for different situations.
RATING: 4

Palmer, M.W. (1990). **The estimation of species richness by extrapolation**. *Ecology* 71, 1195–1198.
A nice concise paper (only 4 pages) providing a brief overview of estimators. The paper breaks down estimators into 4 different categories and measures their performance on data where the "true" species richness is known. It found all eight estimators tested were biased. Six underestimate and two overestimate species richness. The first-order jackknife estimator was the most precise and least biased.
RATING: 4

Ulrich Brose, Neo D. Martinez, and Richard J. Williams. 2003. **Estimating species richness: sensitivity to sample coverage and insensitivity to spatial patterns.** *Ecology* 84: 2364–2377.
A broad estimate of 11 different richness estimators.
This paper examines the some of the factors influencing the accuracy of species richness estimators. They look at different landscapes that varied in species richness, relative abundances, and in spatial distribution. One finding was that nonparametric estimators were much less biased and more precise than species accumulation curves. Species richness estimation depends on the relative abundance distribution and sampling intensity and not so much on spatial patterns. The paper recommends researchers base estimator choice on the mean estimated sample coverage by many different estimators. The paper also gives a good graphical guide of choosing most appropriate estimator.
RATING: 4

Hellmann, J.J. and G.W. Fowler. 1999. **Bias, precision, and accuracy of four measures of species richness.** *Ecological Applications* 9:824-834.
Comparison of jackknife and bootstrap with some good definitions.
This paper compares jackknife and bootstrap estimators and the effect of sample size on estimator performance. Results from least biased estimator to most biases were second-order jackknife, first-order jackknife, bootstrap and lastly simple species richness. Overall, this paper was okay. I am listing it because it has good definitions of Bias (Does the estimator chosen systematically over or underestimate species richness?), precision (If the estimation procedure were repeated a second time, would the second answer be similar to the first?) and accuracy (How close to the true species richness value is the richness estimate?).
RATING: 3

Mao, C. X., and R. K. Colwell. 2005**. Estimation of species richness: mixture models, the role of rare species, and inferential challenges.** *Ecology* 86:1143-1153
A very recent paper looking at the role of rare species.
This is a recent paper painting a rather pessimistic view of species richness estimation. It looks at the role of rare species and why these make richness estimation so difficult. Lots of juicy equations in here for you math folks.
RATING: 3

Schneider, K., and D.C. Culver. 2004. **Estimating subterranean species richness using intensive sampling and rarefaction curves in a high density cave region in West Virginia.** *Journal of Cave and Karst Studies* 66:39-45.
Despite this is a little known journal in our world, it is a nice little study showing the use of the species accumulation curve in biodiversity mapping while using rarefaction and Chao estimate to give species estimates. But only should be read after reading everything else.
RATING: 3

Tipper, J.C., 1979. **Rarefaction and rarefiction - the use and abuse of a method in paleontology.** *Paleobilogy* 5: 423-434.
The best title in this bibliography which has a good overview of Rarefaction, but it's a bit outdated.
This paper gives a nice history up to 1977 of the history and fighting over rarefaction and gives a nice basic overview. It goes over the assumptions and formulas and in the ends recommends against (the rarefiction part) using it and instead using direct comparisions of abundance distributions using a two-sided Smirnov test.
RATING: 2

Willott, S. J. 2001. ***Species accumulation curves and the measure of sampling effort.*** *Journal of Applied Ecology* 38(2):485-487.
A nice short paper that highlights the importance of choosing the correct sampling effort required when constructing a species accumulation curve. This paper critiques a paper (Moreno & Halffter, 2000) which, according to Willott, used an incorrect sampling regime for what was being sampled.
RATING: 2

Moreno, C. E., and G. Halffter. 2001. **On the measure of sampling effort used in species accumulation curves.** *Journal of Applied Ecology* 38: 487-490.
And to show that there is no major agreement among ecologists on this topic, this is a response to the Willott (2001) paper saying, no, we had it right the first time.
RATING: 1

Sanders, H. L. 1968. **Marine benthic diversity: a comparative study**. *American Naturalist.* 102:243-282.
The original rarefaction formula came from this paper though I have not read it.

Efron, B., & Thisted, R. (1976). **Estimating the number of unseen species: How many words did Shakespeare know?** *Biometrika, 63*, 435-447.
Where the analogy used in our discussion highlighting the difficultly of estimation. The analogy of trying to estimate the total vocabulary of a writer from the given sample of his or her recorded works.

A very nice read in plain english:

Magurran, A. E. 1988. **Ecological diversity and its measurement.** Princeton University Press, Princeton, N.J.

SOFTWARE

Gotelli & Entsminger (2001) **Esosim null model software for ecology, Version 6.0.**
http://homepages.together.net/~gentsmin/ecosim.htm
This is software that can be used to construct rarefaction curves (with confidence intervals) when sampling is individual based.

EstimatesS will also calculate sample based rarefaction among other things.