THE INVENTORY AND ESTIMATION OF PLANT SPECIES RICHNESS

A. Chiarucci

Dipartimento di Scienze Ambientali, Università di Siena, Italy

M.W. Palmer

Botany Department, Oklahoma State University, USA

Keywords: Biodiversity, species richness, estimation, jackknife, bootstrap

Contents

- 1. Introduction
- 2. Species Inventorying
- 2.1. Traditional Collection of Species Data
- 2.2. Methods for Perfecting Species Lists
- 3. Estimating and comparing species richness through samples
- 3.1. Fitting Species Abundance Distributions
- 3.2. Estimation Derived from Species Accumulation Curves and Species Area Curves
- 3.3. Non-parametric Estimators

3.4. Taxon-surrogacy and Higher-taxon Approaches

- 4. Conclusion
- Glossary
- Bibliography
- **Biographical Sketches**

Summary

In this chapter we discuss first the techniques which are traditionally adopted by botanists for compiling species lists in areas larger than size which can completely be censused, evidencing the limitation and the possible way to improve them. Useful tools for improving specie lists may derive from the use of environmental information based on geographical information systems, which can direct the new effort in searching plant species. In the following section we discuss the different strategies for estimating and comparing species richness through samples. These methods are classified into three groups. The first group relies on the integrating the species abundance data to a given distribution and estimating how many species were unsampled. In the methods belonging to the second group, the estimated values of species richness are derived from species accumulation curves - in which the pooled number of species is given function of number of sample - and species area curves - in which the pooled number of species is given function of total area sampled. The third group of methods is based on the use of nonparametric estimators which provide an estimate of total species richness of the investigated community based on incidence (presence/absence) or abundance (number of individuals) values of species observed in the sample. Finally some considerations on the use of *taxon* surrogacy techniques, which provide an estimate of species richness of a given taxonomic group based on data of another taxonomic group.

1. Introduction

The assessment of species diversity has been central to plant ecology for a long time (Arrhenius, 1921; Gleason, 1922; Peet, 1974; Magurran, 1988). Species diversity is one of the components of biodiversity (Wilson 1988) and, although the inventorying of global species is far from complete, species diversity is often the most convenient 'proxy' for other components of biodiversity, such as genetic diversity and landscape diversity. However, the taxonomic knowledge is unbalanced among different groups, providing some difficulty in the assessment of species richness. Gaston & May (1992) estimated that on average, vertebrates received 10 times more taxonomic effort than plants and 100 times more effort than invertebrates. The situation for fungi and other groups is likely to be even worse. Recently, growing concern about the loss of biodiversity caused by human activities led to new challenges for the development of powerful and affordable methods for quantifying species diversity, in order to monitor and predict the erosion of biodiversity caused directly or indirectly by human activities. The need to assess such changes in biodiversity has given a sense of urgency for basic and applied research in species diversity. Since it is not possible to monitor all the components of species diversity at broad spatial scales, its estimation by indirect methods is receiving much current attention. However, these methods have not yet been adequately evaluated (Colwell & Coddington, 1994).

Species diversity can be partitioned into two components: richness and evenness. The concept of species richness is one of the oldest and most fundamental in community ecology (Hutchinson 1959, Whittaker 1965, Peet, 1974; Magurran, 1988; Gotelli & Colwell, 2001). Many authors have reported the significant effects of species richness on important ecological processes such as ecosystem productivity and stability (Tilman & Downing, 1994; Naeem et al., 1994; Loreau, 2000); this work remains controversial (Aarsen, 1997). Complementarity is another important concept which is used to measure distinctness or dissimilarity between species assemblages (Colwell & Coddington, 1994). Species richness and complementarity represent the most significant components of biodiversity for evaluating and monitoring purposes, also in landscape contexts (Colwell & Coddington, 1994; Gaston, 1996). Most techniques to estimate species richness do not require any fundamental assumptions about community or landscape structure (Colwell & Coddington, 1994), and can be used as independent tools to assess and monitor the effects on species composition and diversity of management practices, which are often planned on a different basis (e.g. by managing vegetation structure according to a map of habitat types). Moreover, the maximization of species richness represents one of the most important goals for the design of reserves and reserve networks, and the maintenance of native species diversity is a frequent goal of conservation. Thus, the inventory of species and the quantification of species richness represent important steps both in pure and applied plant ecology.

In this chapter we discuss current techniques for evaluating species richness and carrying out species lists as completely as possible. We do not address the problems connected with measuring evenness and diversity indices. The problems involved in inventorying species in small areas are qualitatively similar to those in large areas, although inventories of smaller areas are more likely to be complete for a fixed amount of effort.

Progress in perfecting species lists and estimating species richness at the "park size" units would be very useful because decisions on land use and conservation of biodiversity are often made on these scales (Palmer 1991, Colwell & Coddington, 1994; Gaston, 1996). We first discuss how species lists are traditionally compiled, with their advantages, limitations and future promise, then we discuss different strategies for estimating species richness (i.e. based on fitting species abundance distributions, by extrapolating form species accumulation curves and species-area curves and by using non parametric estimators), and finally we briefly consider the use of *taxon* surrogacy techniques.

2. Species Inventorying

2.1. Traditional Collection of Species Data

The most traditional approach to inventorying the plant diversity of a given area - e.g. a bog, a nature reserve or a province - consists of the preparation of floristic lists, also known as *floras*. The term 'flora' has been variously defined, but here we follow Lawrence (1951): "the inventory of all the plant species recorded for a given site". Floras are extremely useful as basic data, to analyze ecological processes (e.g. gradients over countries), to evaluate the biogeographic significance of nature reserves, parks and geographic or administrative units, to test specific hypotheses on speciation and spreading of plant groups, and to evaluate the factors controlling species diversity. A large amount of such data is available for many countries, often from a long time ago. This type of information also represents an important source for analyzing and understanding ecological processes over long periods.

Although some authors have tried to provide some standards for the writing of a flora (e.g. Palmer et al., 1995), there is no general consensus on the rules to be followed. A floristic inventory may be circumscribed to some taxonomic groups of plants (e.g. phanerogams or bryophytes), as well as to artificial groups (e.g. tree species or medicinal plants) and may contain different types of information. Some authors prefer to limit the term "flora" only to comprehensive works that include species descriptions and identification keys for large regions, differentiating them from less comprehensive species lists of smaller regions named checklists, species inventories or species lists.

Floristic lists are normally compiled by subjectively searching for and collecting plants, trying to obtain a list of species as complete as possible. Usually, the searching strategy simply follows the "botanic internal algorithm", which consists of a combination of ability, experience, expertise and intuition (Palmer et al., 2002). This strategy of plant collection consists of visiting unusual habitats, edges between vegetation types, geomorphic or geologic anomalies, which can lead to the finding of many rare or infrequent species, and thus to a rich list of species. The resulting floras are extremely variable in the amount and the quality of the data provided, depending on the abilities and expertise of the botanists as well as on the time invested.

2.2. Methods for Perfecting Species Lists

Even though it may be impossible to assess the completeness of a flora, quantitative methods coupling floristic data with geographic information systems (GIS) can assist a botanist in completing species lists (Palmer et al., 2002). For example, a GIS derived from ecologically meaningful data layers (e.g. topography, land use, soil type, vegetation type, remote imagery) can produce maps of 'environmental unusualness' that would guide the botanist to interesting habitats. Other useful maps may indicate regions that are most dissimilar to already studied regions.

The measure of unusualness may be an intrinsic property of the points included into the study area (given the average condition of the area) as well as relative to the environments which have been already explored from a floristic point of view.

Regression models can produce maps of predicted species richness, based on variables that have been found to be correlated to species richness, and hence alert the botanist to potential biodiversity "hotspots". Similar models can point out regions that have been largely understudied. Ideally, the methods described above can be employed in an iterative manner: e.g. as an area becomes better understood, the maps of predicted new records and biodiversity hotspots will become perfected.

3. Estimating and Comparing Species Richness through Samples

The complete listing of species is a rather difficult, if not impossible, task even for well known groups such as vascular plants. Complete field surveys are impossible for large areas. When compiling a flora, many botanists apply a personal evaluation, based on their experience, to perceive when they have to stop plant collection since "there are not" (or perhaps "there should not be") additional species to be found, or that the perceived payoff in "new species" is not worth the additional effort. For larger areas, like nature reserves, provinces or states, it is unlikely that we will ever obtain complete lists of species, because botanists cannot explore every square centimeter of the regions searching for the "missing" species (Palmer, 1995; Gaston, 1996; Palmer et al., 2002). Moreover, the species present within a site change through time (e.g. McCollin et al., 2000), and the species-time relationships over ecological time have only seldom taken into account (Gaston, 1996). The amount of time needed for collecting specimens to perform "complete lists" of large regions increases the possibility of including a part of this temporal change, inducing a high risk of taking a "blurred photograph" of the species assemblage. In addition, it is almost impossible to evaluate the completeness of species lists (Palmer, 1995; Gaston, 1996), since quantitative tools to assess subjective factors (such as botanical expertise and effort) are not easy to use.

It is clear that if we are interested in evaluating and monitoring species richness, in a site larger than several thousand square meters, we need to approach the problem by statistical sampling and not by complete survey (Colwell & Coddington, 1994). In addition, if monitoring programs are implemented, it is important to develop powerful methods to estimate species richness objectively with a limited number of samples, and to develop tools to statistically compare samples in different regions or times.

Different methods have been proposed for estimating the number of species from sampling data, mostly belonging to three distinct classes of approach (Palmer, 1990;

Colwell & Coddington, 1994; Palmer, 1995): the first class estimates the number of species based on fitting species abundance data to a known parametric distribution; the second class lies on extrapolation of species richness from species-accumulation functions; the third group approaches the problem by nonparametric estimators based on incidence data (presence/absence) or abundance data. A fourth approach relies on the uses of taxon surrogacy or indicator groups, *i.e.* the use of one, or more than one, taxonomic group for estimating the number in another group.

3.1. Fitting Species Abundance Distributions

This group of methods for estimating species richness is based on the assumption that the number of species is related to the species abundance distribution, a topic that has a deep history in ecological theory (Preston 1948, May 1988, Rosenzweig 1995, Hubbell 2000). If it is possible to characterize the abundance distribution based on a limited number of parameters, then it should be possible to estimate the total number of species (Preston, 1948; Pielou, 1975; Miller & Wiegert, 1989). The distributions most commonly used in ecology are the log-series (Williams, 1964), lognormal (Preston, 1948; Sugihara, 1980), and Poisson lognormal (Bulmer, 1974). For fitting species abundance models to parametric distributions, species abundance should be sampled in a manner consistent with the theory. The matching of a model with data is not a trivial issue, as ecologists measure abundance in many different ways (e.g. density, biomass, cover and frequency; see e.g. Moore & Chapman, 1986) each with a potentially different abundance distribution. Typically, the number of individuals (i.e. density) is considered the appropriate measure of species abundance for calculating abundance distribution. However, this is infeasible in most plant communities, since the clonal nature of many plants makes the identification of 'individuals' difficult. The distinction between genetic individuals (genets) and physiological individuals (ramets) can be arbitrary, given the frequency of vegetative propagules, apomixis, and somatic mutation in plants. Some authors (e.g. Palmer, 1990) used species cover as measure of species abundance for calculating abundance distribution, but a sound theoretical basis for connecting species cover or other measures to the density is still missing (but see Mouillot et al. 2001 for a promising approach). Other authors (e.g. Zobel & Liira, 1997) have used ramet (shoot) density for standardizing species richness samples instead using physiological individuals.

Some authors have suggested that the integration of the lognormal distribution of species abundances is a powerful method for estimating species richness (Preston, 1948; Slocomb & Dixon, 1978, Miller & Wiegert, 1989). The "canonical" log-normal distribution of species abundance was introduced by Preston (1948; 1962) and it is usually written in the form:

$$S(R) = S_{\text{oct}} e^{-(aR)^2}$$

where species abundances are transformed on a \log_2 basis and the resulting classes are termed octaves. S(R) is the number of species in the R^{th} octave to the right and left of the modal octave; S_{oct} is the number of species in that modal octave, and *a* is the inverse width of the distribution $[a=1/(2\sigma^2)^{1/2}]$. The parameter *a* represents a measure of the equitability of species abundance in the community, being known to be about 0.2 in

natural communities (Preston, 1962, Sugihara, 1980; Baltanás, 1992). This parameter usually shows a decrease with the increase of individuals sampled (Preston, 1962).

Once the distributions parameters (S_{oct} and a) are known, the total number of species expected on the basis of the assumptions of this model can be calculated by:

$$S = S_{\rm oct} \sqrt{\pi/a}$$

Figure 1 shows the canonical distribution of species abundance as reported by Preston (1962), with the coefficient a = 0.200, the modal frequency $S_{\text{oct}} = 20$ species and the standard deviation $\sigma = 3.53$ octaves.

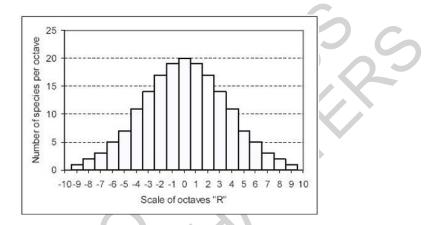


Figure 1. Canonical distribution of species abundance in a community of 178 species (theoretical not empirical) as originally reported the Preston (1948). For this number of species the coefficient a = 0.200 and the standard deviation σ is 3.53 octaves; the modal frequency is $S_{oct} = 20$ species.

Of course, the distribution is normally obtained by a finite sample, and the less abundant species are usually missing from it. The resulting distribution is said to be truncated on the left side and it is necessary to integrate a Gaussian curve to estimate how many species were unsampled on the left tail. This method, as well as all the other distribution-fitting methods, is based on the strict assumption that the number of species is a function of parametric distribution of species abundance (true lognormal in this case). The observed abundance values of each species are then fitted to this theoretical model of expected frequency for each abundance class.

Slocomb & Dixon (1978) found that that lognormal method might provide unreliable estimates of species richness unless the sample size is very high and the number of species in the sample is more than 80% of the total number of species in the whole community. In a simulation, Baltanas (1992) observed that the estimation based on the Cohen (1959; 1961) method, i.e. a maximum likelihood method for fitting lognormal distribution, achieved the best precision with respect to other nonparametric estimators and extrapolation for species-area curves (discussed later). However, it should be remarked that this author evaluated these methods based on simulated abundances derived from the lognormal distribution. Thus, the lognormal method is predisposed to work well with such artificial data, perhaps in contrast to real data that may

substantially diverge from typical lognormal distributions. In fact, although some studies have found that the values observed in nature for species abundance distribution were rather consistent with the lognormal distribution (e.g. Schmit et al., 1991 for fungi), the consistency between species abundance and the lognormal distribution is not necessarily true, making somehow inconsistent the estimation of species richness by using this approach. Hubbell (2000) presents some theoretical arguments that real abundance distributions will have a substantially fatter left tail than the lognormal distribution, and hence methods based on integrating the lognormal curve will underestimate the true richness.

- -
- -

TO ACCESS ALL THE **23 PAGES** OF THIS CHAPTER, Visit: <u>http://www.eolss.net/Eolss-sampleAllChapter.aspx</u>

Bibliography

Aarsen L.W. (1997). High productivity in grassland ecosystems: affected by species diversity or productive species? *Oikos* 80, 183-184. [an attempt to quantify the role of species diversity to ecosystem functioning]

Arrhenius O. (1921). Species and area. *Journal of Ecology* 9, 95-99. [One of the first studies investigating the species-area relations]

Bakker J.P., Olff H., Willems J.H., Zobel M. (1996). Why do we need permanent plots in the study of long-term vegetation dynamics?. *Journal of Vegetation Science* 7: 147-156. [a perspective on the need of establishing permanent plots for studying vegetation and ecosystem dynamics]

Baltanás A. (1992). On the use of some methods for the estimation of species richness. *Oikos* 65, 484-492. [An investigation of the performance of different methods for estimating species richness]

Bulmer M.G. (1974). On fitting the Poisson lognormal distribution to species abundance data. *Biometrics* 30, 101-110. [A study concerning the fitting the Poisson lognormal distribution to species abundance data in communities]

Bunge J., Fizpatrick M. (1993). Estimating the number of species: a review. *Journal of the American Statistical Association* 88, 364-373. [A fundamental paper on the estimation of species richness in communities]

Burnham K.P., Overton W.S. (1978). Estimation of the size of a closed population when capture probabilities vary among animals. *Biometrika* 65, 623-633. [A study of methods for estimating population size based on capture-recapture techniques when not all the species have the same probability to be captured]

Burnham K.P., Overton W.S. (1979). Robust estimation of the size of population size when capture probabilities vary among animals. *Ecology* 60, 927-936. [A study of methods for estimating population size based on capture-recapture techniques when not all the species have the same probability to be captured]

Chao A. (1984). Nonparametric estimation of the of classes in a population. *Scandinavian Journal of Statistics* 11, 265-270. [A paper in which an estimator of species richness based on the number of individuals of the rarest species is proposed]

Chao A. (1987). Estimating the population size for capture-recapture data with unequal catchability.

Biometrics 43, 783-791. [A paper in which the formulae for the variance of Chao1 and Chao2 estimators are provided]

Chao A., Lee S.-M. (1992). Estimating the number of classes via sample coverage. *Journal of the American Statistical Association* 87, 210-217. [A paper presenting the use of richness estimators based on the statistical concept of "sample coverage"]

Chao A., Ma M.C., Yang M.C.K. (1993). Stopping rules and estimation for recapture debugging with with unequal failure rates. *Biometrika* 80, 193-201. [A discussion of richness estimators based on the abundance of the rarest species]

Chazdon R.L., Colwell R.K., Denslow J.S., Guariguata M.R. (1998). Statistical methods for estimating species richness of woody regeneration in primary and secondary rain forests of NE Costa Rica. In: Dallmeier F., Corniskey J. (eds.), *Forest biodiversity in North, central and South America and the Caribbean: research and monitoring*. Parthenon Publishing, Paris, pp. 285-309. [An application to ecological data of nonparametric estimators with general discussion]

Chiarucci A., Maccherini S., De Dominicis V. (2001). Evaluation and monitoring of the flora in a nature reserve by estimation methods. *Biological Conservation* 101, 305-314. [A field test of the performance of different estimators of species richness using plant species]

Clench H. (1979). How to make regional lists of butterflies: some thoughts. *Journal of the Lepidopterist's Society* 33, 216-231. [An investigation of regional species richness of butterfly by the application of the Michaelis-Menten equation of enzyme kinetics]

Cohen A.C.J. (1959). Simplified estimators for the normal distribution when samples are singly censored or truncated. Technometrics 1, 217-237. [A paper presenting a likelihood method for fitting lognormal distribution]

Cohen A.C.J. (1961). Tables for maximum likelihood estimates: singly truncated and singly censored samples. *Technometrics* 3, 535-541. [A paper presenting a likelihood method for fitting lognormal distribution]

Coleman B.D. (1981). On random placement and species-area relations. *Mathematical Biosciences* 54, 191-215. [A paper discussing the "random placement curve" and the species-area realtions]

Coleman B.D., Mares M.A., Willig M.R., Hsieh Y.H. (1982). Randomness, area, and species richness. *Ecology* 63, 1121-1133. [A paper discussing the "random placement curve" and the species-area realtions]

Colwell R.K., Coddington J.A. (1994). Estimating terrestrial biodiversity through extrapolation. *Philosophical Transactions of the Royal Society of London*, Series B 345, 101-118. [A review of the different methods adopted for estimating species richness]

Connor E.F., McCoy E.D. (1979). The statistics and biology of the species-area relationships. *American Naturalist* 113, 791-833. [a fundamental paper investigating the performance of different models of species-area relations]

De Capraris P., Lindemann R.H., Collins C.M. (1976). A method for determining optimum sample size in species diversity studies, *Journal of the International Association for Mathematical Geology* 8, 575-581. [A proposal for a statistical determination of optimum sample size in studies of species diversity]

Dony J.G. (1977). Species-area relationships in an area of intermediate size. Journal of *Ecology* 65, 475-484. [A paper on species-area curves]

Engen S (1978). *Stochastic abundance models*. Chapman & Hall, London, UK. [A statistical book related to stochastic processes in abundance models]

Forbes S., Schauwecker T., Weiher E. (2001). Rarefaction does not eliminate the species richnessbiomass relationships in calcareous blackland prairies. *Journal of Vegetation Science* 12, 525-532. [An investigation of the effects of plant density on the species richness – biomass relationships in grasslands]

Gaston K.J. (1996). *Species richness: measure and measurement*. In Gaston, K.J. (ed.), *Biodiversity. A biology of numbers and differences*. Blackwell Science, pp.77-113. [A general introduction on the issues of species richness and its measurement]

Gaston K.J., May R.M. (1992). The taxonomy of taxonomists. *Nature*, 356: 281-282. [A study investigating the efforts done by taxonomy and taxonomists to classify biological diversity]

Gaston K.J., Williams P.H. (1993). Mapping the world's species: the higher taxon approach. *Biodiversity Letters*, 1, 2-8. [A large-scale study of using the higher-taxon approach for quantifying and mapping species richness]

Gimaret-Carpentier C., Péllissier R., Pascal J.P., Houllier F. (1998). Sampling strategies for the assessment of tree species diversity. *Journal of Vegetation Science* 9, 161-172. [A study proposing efficient vegetation sampling strategies by different sampling designs and choice of species richness estimators]

Gitay H., Roxburgh S.H., Wilson J.B. (1991). Species-area relations in a New Zealand tussock grassland, with implications for nature reserve design and for community structure. *Journal of Vegetation Science* 2, 113-118. [A field study of species-area relationships, introducing a new model and providing larger-scale extrapolations]

Gleason H.A. (1922). On the relation between species and area. *Ecology* 3, 158-162. [One of the first studies investigating the species-area relations]

Gotelli N.J., Colwell R.K. (2001). Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecology Letters* 4, 379-391. [An up-to-date review of the issues and problems related to the rarefaction methods for quantifying species richness]

Good I.J. (1953) The population frequencies of species and the estimation of population parameters. *Biometrika* 40, 237-264. [A paper on the effects of species distribution on the estimation of population parameters]

Harris B. (1959). Determining the bounds on integrals with applications to cataloging problems. *Ann. Math. Statist.* 30, 521-548. [A statistical proposal for determining the bounds in integral inventorying]

Hawksworth D.L. (1991). The fungal dimension of biodiversity: magnitude, significance, and conservation. *Mycological Research* 95: 641-655. [A review of the fungal biodiversity]

Hellmann J.J., Fowler G.W. (1999). Bias, precision, and accuracy of four measures of species richness. *Ecological Applications* 9, 824-834. [A field test of the performance of different estimators of species richness]

Heltshe J.F, Forrester N.E. (1983). Estimating species richness using the Jackknife procedure. *Biometrics* 39, 1-11. [The first proposal to use a Jackknife procedure to estimate species richness]

Holdridge L.R., Grenke W.C., Hatheway W.H., Liang T., Tosi J.A. (1971). *Forest environments in tropical life zones*. Pergamon Press, Oxford. [One of the first examples of using an asymptotic curves for estimating species richness]

Hutchinson G.E. (1959). Homage to Santa Rosalia, or, why are there so many kinds of animals? *American Naturalist* 93, 145-159. [A famous lecture gave by G.E. Hutchinson discussing the species richness issue and representing one of the starting points of the species diversity modern literature]

Keating K.A., Quinn J.F. (1998). Estimating species richness: the Michaelis-Menten model revisited. *Oikos* 81, 411-416. [A discussion on the use of the Michaelis-Menten model for estimating species richness in communities]

Kilburn P.D. (1966). Analysis of the species-area relation. *Ecology* 47, 831-843. [A study of species-area relations]

Lawrence G.H.M. (1951). *Taxonomy of vascular plants*. Macmillan Co., New York. [a book on the taxonomy of vascular plants]

Lee S.M., Chao A. (1994). Estimating population size via sample coverage for closed capture-recapture models. *Biometrics* 50, 88-97. [A paper presenting the use of richness estimators based on the statistical concept of "sample coverage"]]

Loreau M. (2000). Biodiversity and ecosystem functioning: recent theoretical advances. *Oikos* 91: 3-17. [a study on the relationships between biodiversity and ecosystem functioning]

Magurran A.E. (1988). Ecological diversity and its measurement. Chapman and Hall, London. [a

fundamental book on species diversity and its measurements]

May, R. M. (1988). How many species are there on Earth? *Science* 241, 1441-1449. [an attempt to provide estimates of the number of specie present on the Earth]

McCollin D., Moore L., Sparks T. (2000). The flora of a cultural landscape: environmental determinants of change using archival sources. *Biological Conservation* 92, 249-263. [A floristic study discussing the issue of temporal changes in the flora]

Miller R.J., Wiegert R.G. (1989). Documenting completeness, species-area relations, and the speciesabundance distribution of a regional flora. *Ecology* 70, 16-22. [A paper suggesting the integration of the lognormal distribution of species abundances as a method for estimating species richness]

Moore P.D., Chapman S.B. (1986). *Methods in plant ecology*. Blackwell Scientific Publications, Oxford. [A plant ecology textbook]

Mouillot D., Culioli J.-M., Wilson J.B., Frodello J.-P., Mouillot F., Leprêtre A., Marchand B. (2001). Number, length, area or biomass: can there be intermediates? *Écoscience* 8, 264-7. [A paper discussing the problems concerning the measurement of plant density in local assemblages]

Naeem S., Thompson L.J., Lawler S.P., Lawton J.H., Woodfin R.M. (1994). Declining biodiversity can alter the performance of ecosystems. *Nature* 368, 734-736. [A paper investigating the functional role of biodiversity on ecosystem functioning]

Palmer M.W. (1990). The estimation of species richness by extrapolation. *Ecology* 71, 1195-1198. [A field test of the performance of different estimators of species richness using plant species]

Palmer M.W. (1991). Estimating species richness: the second-order jackknife reconsidered. *Ecology* 72, 1512-1513. [A correction of the results reported in the above cited paper]

Palmer M.W. (1995). How should one count species? *Natural Areas Journal* 15, 124-135. [a review of the methods for counting and estimating the number of plant specie within an area]

Palmer M.W., Earls P.G., Hoagland B.W., White P.S., Wohlgemuth T. 2002. Quantitative tools for perfecting species lists. *Environmetrics* 13, 121-137. [a review of the methods usable for estimating detecting how many species are missing from species lists and locating where they can be sampled]

Palmer M.W., Wade G.L., Neal, P., (1995). Standards for the writing of floras. *BioScience* 45, 339-345. [an attempt to provide standards for the writing of floras]

Palmer M.W., White P.S. (1995). On the existence of ecological communities. *Journal of Vegetation Science* 5, 279-282. [A discussion on the nature of ecological communities as artificial or natural entities]

Peet R.K. (1974). The measurement of species diversity. *Annual Review of Ecology and Systematics* 5, 285-307. [A review of the problems and methods for measuring species diversity within communities and landscapes]

Pharo E.J., Beattie A.J., Binns D. (2000). Vascular plant diversity as a surrogate for bryophyte and lichen diversity. *Conservation Biology* 13, 282-292. [A field study of the relations between the species richness of vascular plants and that of cryptogams – bryophytes and lichens]

Pharo E.J., Beattie A.J., Pressey R.L. (2000). Effectiveness of using vascular plants to select reserves for bryophytes and lichens. *Biological Conservation* 96, 371-378. [A field study of the effectiveness of using species richness of vascular plants o select nature reserves for cryptogams – bryophytes and lichens]

Pielou E.C. (1975). *Ecological diversity*. Wiley Interscience, New York, USA. [A fundamental book on mathematical aspects of ecological diversity]

Preston F.W. (1948). The commonness and rarity of species. *Ecology* 29, 254-283. [A fundamental paper on the species distribution frequency]

Preston F.W. (1962). The canonical distribution of commonness and rarity. *Ecology* 43, 185-215. [A discussion of species abundance distribution with discussion on its potential application for estimating species richness]

Ryti R.T. (1992) Effect of the focal taxon on the selection of nature reserves. *Ecological Applications* 2, 404-410. [An investigation of the effects on total species richness of the selection of nature reserves based

on a focal taxon]

Schreuder H.T., Williams M.S., Reich R.M. (1999). Estimating the number of tree species in a forest community using survey data. *Environmental Monitoring and Assessment* 56, 293-303. [A study on species richness estimation based on the use of samples composed by true individuals]

Schmit J.P., Murphy J.F., Mueller G.M. (1999). Macrofungal diversity of a temperate oak forest: a test of species richness estimators. *Canadian Journal of Botany* 77: 1014-1027. [A field test of the performance of different estimators of species richness using fungal species]

Simberloff D. (1979). Rarefaction as a distribution-free method of expressing and estimating diversity. In Grassle J.F., Patil G.P., Smith W.K., Taillie C (eds.) *Ecological diversity in theory and practice*. Pp. 159-176. International Cooperative Publishing House, Fairland, Maryland, USA. [Description of the advantages of using rarefaction methods for estimating species diversity]

Skow F., Lawesson J.E. (2000). Estimation of plant species richness from systematically placed plots in a managed forest ecosystems. *Nordic Journal of Botany* 20, 477-483. [A field test of the performance of different estimators of species richness using plant species]

Slocomb J., Dickson K.L. (1978). Estimating the total number of species in a biological community. In Dickson K.L., Cairns Jr. J., Livingston R.J. (eds.), Biological data in water pollution assessment: quantitative and statistical analyses. American Society for testing and materials, Philadelphia, PA, pp. 38-52. [A discussion of the possible methods to be used for estimating species richness in communities]

Smith E.P., van Belle G. (1984). Nonparametric estimation of species richness. *Biometrics* 40, 119-129. [A paper introducing a bootstrap method for estimating species richness]

Sugihara G. (1980). Minimal community structure: an explanation of species abundance patterns. *American Naturalist* 116, 770-787. [A description and interpretation of species abundance distribution in natural communities]

Tardif B., DesGranges J.-L. (1998). Correspondence between bird and plant hotspots of the St. Lawrence River and influence of scale on their location. *Biological Conservation*, 84 53-63. [a study on the spatial covariance of species richness of plants and birds in order to detect potentially usable relations]

Tilman D., Downing J.A. (1994). Biodiversity and stability in grasslands. *Nature* 367: 363-365. [a study on the relationships between species diversity and community stability]

Tipper J.C. (1979). Rarefaction and rarefiction - the use and the abuse of a method in paleoecology. *Paleobiology* 5, 423-434. [Description of the advantages of using rarefaction methods for estimating species diversity]

Whittaker R.H. (1965). Dominance and diversity in land plant communities. *Science* 147, 250-260. [One of the first study on the ecological meaning of the species abundance distribution]

Williams C.B. (1964). *Patterns in the balance of nature*. Academic Press, London, UK. [A basic book including description of basic characteristics of species abundance distributions]

Williams P.H., Gaston K.J. (1994). Measuring more of biodiversity: can higher taxon richness predict wholesale species richness? *Biological Conservation*, 67 211-217. [A study proposing the use of richness in taxa of higher level as a measure of species richness]

Williamson M., Gaston K.J., Lonsdale W.M. (2001). The species-area curve does not have an asymptote! *Journal of Biogeography* 28, 827-830. [A paper on the non-asymptotic nature of species-area curves]

Wilson J.B., Chiarucci A. (2000). Forum: Do plant communities exist? Evidence from scaling-up local species-area relations to the regional level. Journal of Vegetation Science 11, 773-775. [a investigation on the consequence on community concept of using estimates from locally derived species-area relations to larger scale]

Wilson, E.O. (ed.) (1988). *Biodiversity*. National Academy Press, Washington, DC. [a fundamental text on conceptual and practical issues of biodiversity]

Zelmer D.A., Esch G.W. (1999). Robust estimation of parasite component community richness. *Journal of Parasitology* 85, 592-594. [A test of the performance of different estimators of species richness using parasites]

Zobel K., Liira J. (1997). A scale-independent approach to the richness vs biomass relationship in groundlayer plant communities. *Oikos* 80, 325-332. [an attempt to provide scale-independent measures of species richness in plant communities, by standardizing to a common number of individuals]

Biographical Sketches

Alessandro Chiarucci is Associate Professor at the University of Siena with interests in community ecology and biodiversity assessment and conservation. His main research focus is on plant communities. He is currently an Associate Editor of the *Journal of Vegetation Science*.

Mike W. Palmer is Professor of Botany and adjunct Professor of Zoology at the University of Oklahoma State University, with interests in community ecology, ecological theory, fractal geometry and conservation of biodiversity. His two largest projects currently are the Floras of North America Project and the Plant Virus Biodiversity and Ecology project. He is member of the Editorial Board of the journals *Community Ecology* and *Journal of Vegetation Science*.