TRENDS IN THE MEASUREMENT OF ALPHA DIVERSITY IN THE LAST TWO DECADES

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SUMMARY

Recent interest in conservation biology has promoted the study of species diversity and the arising of new methods to measure it. We examined how alpha diversity was studied in articles published in two ecological journals from 1982 to 2002. We found 244 articles that measured alpha diversity, and the number of articles per year increased through time with a higher rate of increase after 1991, The most popular measure of diversity was species richness, but since 1994 the use of richness estimators increased. More papers have been devoted to the study of animals, but when they were grouped into vertebrates and invertebrates, these two groups included fewer articles than plants. For the three groups the number of articles increased through time. An increase was observed in both the number of articles written by authors working in North America and by authors from other regions; however, North American authors wrote the majority of papers. Similarly, the number of studies carried out in North America and in other regions increased through time, but more studies were performed in North America and they increased at a higher rate.

RESUMEN

El interés reciente en biología de la conservación ha fomentado el estudio de la diversidad de especies y el surgimiento de nuevos métodos para medirla. En este trabajo se evalúa la forma en que la diversidad alfa ha sido medida en artículos publicados en dos revistas de ecología de 1982 a 2002. Se encontraron 244 artículos que miden la diversidad alfa, y el número de artículos por año aumenta a través del tiempo con una tasa de incremento mayor después de 1991. La medida más popular de la diversidad es la riqueza de especies, pero desde 1994 se ha incrementado el uso de estimadores de riqueza. La mayoría de los artículos son sobre estudios con animales, pero cuando los dividimos en vertebrados e invertebrados, estos dos grupos incluyen menos artículos que los dedicados a plantas. Para estos tres grupos el número de artículos incrementa en el tiempo. Se observó también un incremento tanto en el número de artículos escritos por autores que laboran en Norte América como por autores que laboran en otras regiones; sin embargo, los autores norteamericanos publican la mayoría de los trabajos. De manera similar, el número de estudios realizados en Norte América y el número de estudios realizados en otras regiones se incrementa a través del tiempo, pero se realizan más estudios en Norte América y estos son publicados a una tasa más elevada.

The study of species diversity in ecological communities has been one of the major topics in ecology in the last decades. It has been approached by analyzing its influence on ecosystem processes such as primary productivity, nutrient cycling, and disturbances; and by measuring how it is affected by ecosystem characteristics such as soil, climate and disturbance regime (Brown *et al*., 2001 and literature cited herein).

Whittaker (1972) proposed a general framework for the study of species diversity by dividing diversity in three main components: alpha diversity, the species richness of a particular habitat considered to be homogeneous; gamma diversity, the species richness of the entire landscape; and beta diversity, the quotient of gamma divided by average alpha, which refers to the species turnover among different habitats in a landscape. Among these components, alpha diversity has received considerable attention, and several reviews have been written in the last decades that summarize the great variety of measures developed to quantify it (Peet, 1974; Pielou, 1975; Washington, 1984; Magurran, 1988, 2004; Colwell and Coddington, 1994; Leitner and Turner, 2001; Chao, 2005).

Two basic types of information may be considered for measuring alpha diversity in ecological communities: species richness and evenness (Gaston, 1996). Evenness refers to differences in species abundance that lead to an unequal representation of species in a community. It is typically evaluated considering the number of dominant

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RESUMO

O interesse recente na biologia da conservação tem fomemtado o estudo da diversidade de espécies e o aparecimento de novos métodos para medi-la. Neste trabalho se avalia a forma em que a diversidade alfa tem sido medida em artigos publicados em duas revistas de ecologia de 1982 a 2002. Encontraram-se 244 artigos que medem a diversidade alfa, e o número de artigos por ano aumenta através do tempo com uma taxa de acréscimo maior despois de 1991. A medida mais popular da diversidade é a riqueza de espécies, mas a partir de 1994 tem se incrementado o uso de estimadores de riqueza. A maioria dos artigos são sobre estudos com animais, mas quando os dividimos em vertebrados e invertebrados, estes dois grupos incluem menos artigos que os dedicados a plantas. Para estes três grupos o número de artigos se incrementa no tempo. Observou-se também, um incremento tanto no número de artigos escritos por autores que laboram na América do Norte como por autores que laboram em outras regiões; no entanto, os autores norteamericanos publicam a maioria dos trabalhos. De forma similar, o número de estudos realizados na América do Norte e o número de estudos realizados em outras regiões se incrementa através do tempo, mas se realizam mais estudos na América do Norte e estes são publicados a uma taxa mais elevada.

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vs the number of uncommon species. Classic indices of diversity combine information of species richness and evenness into one concept called heterogeneity. These diversity or heterogeneity indices like the Shannon-Wiener or the Simpson indices, derived from information theory, are very popular because they are relatively easy to compute, (Krebs, 1999).

Several key meetings and agreements like the US Strategy Conference on Biological Diversity in 1981, the National Forum on BioDiversity in 1986 (Harper and Hawksworth, 1995), the IUBS-SCOPE-UNESCO workshop “From genes to ecosystem: a research agenda for biodiversity” in 1991 (Solbrig, 1991), the Earth Summit and the Convention of Biological Diversity (CBD, signed in 1992 and ratified by the required number of countries in 1993), and the recent interest in conservation biology have generated a strong focus on the impact of human activities on species diversity, and an increasing array of methods to measure it (Krebs, 1999).

Various new approaches to measure diversity have been developed and tested in the last two decades (Magurran, 2004). A big step in the search for better approaches to quantify diversity has been the difference between the number of species recorded in a set of samples, and the estimation of the total possible number of species in a community. Estimation methods are by far more appropriate than indices that measure the diversity of samples, given that, in ecology, the completeness of species inventories is practically an impossible goal. Recent literature has contributed to promote the use of estimation methods by providing or analyzing statistical procedures (Smith and van Belle, 1984; Chao, 1984, 1987, 2005; Soberón and Llorente, 1993; Brewer and Williamson, 1994; Colwell and Coddington, 1994; Lee and Chao, 1994; Chazdon *et al*., 1998; Moreno and Halffter, 2000; Gotelli and Colwell, 2001; Leitner and Turner, 2001; Thompson and Withers, 2003; Thompson *et al*., 2003).

The present paper shows how the analysis of alpha diversity has been done in articles published in two ecological journals (*Ecology* and *Ecological Monographs*) in the last two decades. More specialized journals devoted strictly to publish articles on ecological diversity or conservation, and that in fact include the word biodiversity in their name, appeared in 1992 or later. Thus, given that the trends cannot be analyzed for more than 12 years using biodiversity journals, it was decided to use an ecological journal with a longer history and wide prestige. Among ecological journals, *Ecology* and *Ecological Monographs* differ only in the extent of their articles, but both journals have been published for more than 20 years, and are not restricted to a particular group. Because these two journals are published by the Ecological Society of America, it was also investigated if the articles on alpha diversity in these journals were biased in their geographical scope. These two journals represent only a partial view of the published materials that deal with alpha diversity. Floristic and faunistic lists tend to be published in regional or local journals, theses, or even in museum internal publications, therefore they are spatially restricted and most of the time not available for an unbiased analysis.

The objectives were to evaluate changes through time for the following variables: 1) number of articles analyzing alpha diversity; 2) use of species richness, indices derived from information theory, and richness estimators, as measures of alpha diversity; 3) number of studies that analyze the diversity of major biological groups; 4) number of studies about alpha diversity carried out in the major geographical regions; and 5) number of articles about alpha diversity written by authors working at North American institutions *vs* number of articles written by authors working anywhere else.

Methods

The Institute for Scientific Information's (ISI) data base was consulted to search for all the articles published in *Ecology* and *Ecological Monographs* from 1982 to 2002 that included in their title, or keywords, at least one of the following words: richness, species diversity, and biodiversity.

A preliminary list was obtained including 401 articles from *Ecology* and 76 articles from *Ecological Monographs*. This preliminary list was evaluated in order to identify and delete the references not related to the measurement of alpha diversity.

Each article of our final list was reviewed, and the following variables were recorded: year of publication, methods used to measure alpha diversity (including species richness, heterogeneity indices and richness estimators), author’s country of adscription, biological groups surveyed and geographical region in which the study was done. If a paper reported more than one method, biological group, or study area, or if co-authors had different adscription countries, all the data was considered for the analysis. For example, if an article included two or more study areas in different geographical regions, each region was considered as one different study. Hence, out of the 244 articles considered, 257 studies done in one of the major geographical regions were identified.

Prior to the analyses, the total number of articles per year was counted, including all subjects (4803 articles from 1982 to 2002, $\bar{x}$=229 per year) in order to analyze if the number of published papers in the two journals changed during this period. It was found that the total number of articles had a significant increase through time (r^2=0.73, d.f.=19, P<0.001). Thus, to separate this general tendency of increase in the total number of published papers from the trends being looked for, the proportion of the number of articles about alpha diversity and other variables, out of the total number of articles published per year, was computed. Given that proportions tend to form a binomial distribution, the arcsine transformation (arcsine of the square root of the proportions) was used for the following analyses (Zar, 1999).

A simple linear regression analysis was used to evaluate if the proportion of articles that measure alpha diversity has increased through time. To explore the possible influence of the meetings and agreements mentioned above as representatives of a changing biopolitical landscape, the references were separated in to two periods: from 1982 to 1990, and from 1991 to 2002. The breakpoint for this time separation was arbitrarily fixed *a posteriori* according to a general overview of the results. For both periods simple linear regressions were also performed to see if the proportions of articles were related to time.

To assess the use of different methods to measure alpha diversity through time, three simple linear regressions were computed, having as dependent variables the proportion of articles using 1) species richness, 2) heterogeneity indices, and 3) estimation procedures.

Regression analysis was also used to evaluate the proportion of articles through time devoted to each of the major biological groups (plants, invertebrates, and vertebrates), the proportion of studies done in each geographical region, and the proportion of contributions from authors working in the USA and from authors working in other countries. For these two last variables (study area and author's adscription country) frequencies of the following classes were counted: North America (including USA and Canada), Latin America, Asia, Australia and Europe. Although Mexico is geographically part of North America, it was not included within this area because we believe that language is a major cultural barrier that prevents foreign scientists from doing biological research in Mexico (unless they have a local contact). Additionally, we believe that language is the main reason that prevents Mexican scientists from publishing at the same rate than English speaking scientists, in American or any other English based journal. According to the language affinity, and also because large part of the country is biologically part of Mesoamerica, it was decided to include Mexico in the Latin American region.

All linear regression analyses were performed in Sigma Stat (SPSS, 1997). We compared the slopes of the regression lines for each one of the variables considered, following the procedures described by Zar (1999), t-tests for two slopes and covariance analyses for three or more slopes.

TABLE I
AUTHORS THAT PUBLISHED THREE OR MORE ARTICLES ON ALPHA DIVERSITY, IN THE JOURNALS *ECOLOGY* AND *ECOLOGICAL MONOGRAPHS* (1982 TO 2002)

Author name	Number of articles
J. H. Connell	7
M. R. Willig	5
J. H. Brown	4
J. R. Sauer	4
T. G. Whitham	4
D. S. Hammond	3
J. E. Hines	3
J. D. Nichols	3
S. L. Collins	3
R. H. Karlson	3
M. W. Palmer	3
F. Smith	3
D. Tilman	3

Results

A final list of 244 articles that measured alpha diversity during the 1982-2002 period was obtained, 206 of them published in *Ecology* and 38 published in *Ecological Monographs*. These articles were written by 496 authors. Most authors only wrote one paper during this period, but some authors wrote several articles (Table I).

The proportion of articles analyzing diversity increased significantly through time (Figure 1; r^2=0.68, d.f.=20, P<0.001). When the data set was divided, it was found that the proportion of articles decrease from 1982 to 1990, but this was not significant (r^2=0.06, d.f.=8, P=0.48). However, after 1991 there was a significant increase in the proportion of articles per year (Figure 1; r^2=0.63, d.f.=11, P<0.001). The slopes of these three regressions were statistically different (F=3.96, d.f.=2.38, P<0.05).

The use of species richness (r^2=0.67, d.f.=20, P<0.001), heterogeneity indices (r^2=0.36, d.f.=20, P<0.001) and estimation methods (r^2=0.60, d.f.=20, P<0.001) has increased through time during the last 20 years (Figure 2). Note that in seven years be-

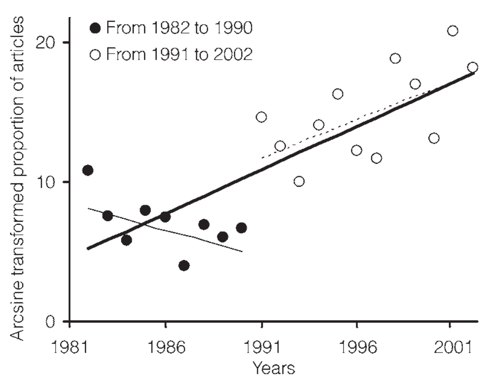

Figure 1. Proportion of articles (arcsine transformed) that measure alpha diversity out of the total number of articles per year published in the journals *Ecology* and *Ecological Monographs* (1982 to 2002), as a function of time. The linear regression is not significant from 1982 to 1990 (thin solid line, r^2=0.06, N=9, d.f.=8, P=0.48), but from 1991 to 2002 the relationship is significant (dashed line, r^2=0.63, N=12, d.f.=11, P<0.001). The linear regression for the entire period (1982 to 2002) is also significant (bold solid line, r^2=0.68, N=21, d.f.=20, P<0.001).

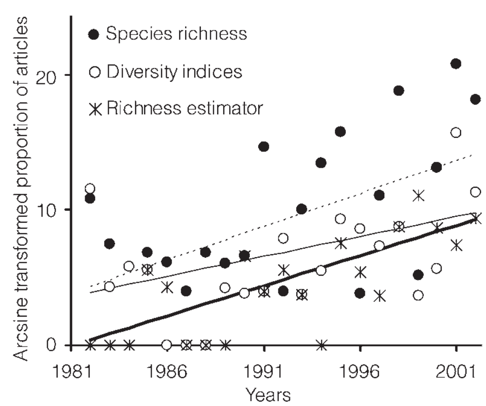

Figure 2. Proportion of articles (arcsine transformed) that used different measures of alpha diversity out of the total number of articles per year published in *Ecology* and *Ecological Monographs* as a function of time. Species richness was more frequently used (dashed line, r^2=0.67, N=21, d.f.=20, P<0.001), followed by diversity indices (thin solid line, r^2=0.36, N=21, d.f.=20, P<0.001), and richness estimators (bold solid line, r^2=0.60, N=21, d.f.=20, P<0.001).

tween 1982 and 1994 these journals did not published any paper using estimation methods. After 1994 at least one paper using richness estimators appeared every year (Figure 2). Species richness has been more popular, followed by heterogeneity indices, and estimation procedures have been less used. However, the slopes of these regression lines were not statistically different (F=0.63, d.f.=3.59, P>0.05).

More studies of alpha diversity done with animals were found (114 articles, 57 devoted to invertebrates and 57 to vertebrates) than with other biological groups: plants (105 articles), prokaryotes (6 articles), and fungi (4 articles). Some papers studied more than one group, and for 20 papers this variable did not apply, eg. theoretical studies. The proportion of articles devoted to plants and animals increased through time (Figure 3; r^2=0.62, d.f.=20, P<0.001 for plants; r^2=0.53, d.f.=20, P<0.001 for invertebrates; r^2=0.53, d.f.=20, P<0.001 for vertebrates). However, there is no statistical difference in the slopes for these three groups (F=0.21, d.f.=2.55, P>0.05).

Of the total, 133 studies were done in North America, 43 in Latin America, 22 in Australia, 15 in Europe, 9 in Asia and 33 were not georreferenced (computer simulated studies). Both the proportion of studies done in North America and the proportion of studies done in all the other countries increased significantly through time (Figure 4; r^2=0.58, d.f.=20, P<0.001 for North America; r^2=0.61, d.f.=20, P<0.001 for the rest of the world). The slope of the regression line was higher for North America than for the rest of the world (d.f.=38, t=2.56, P<0.05).

From the 244 articles, 202 were written by at least one author working in a North American institution, and only 57, by authors from other countries: 24 articles written by authors working in Europe, 16 from Australia, 11 from Latin America, 5 from Asia and 1 from Africa. Both the proportion of articles written by authors working in North American institutions, and the proportion of articles written by authors working in other countries, increased significantly through time (Figure 5; r^2=0.70, d.f.=20, P<0.001 for North America; r^2=0.49, d.f.=20, P<0.001, for the rest of the world), and the increasing rates of these relationships are not statistically different (d.f.=38, t=0.76, P>0.05). However, note that in seven years between 1982 and 1993 these journals did not publish any paper about alpha diversity written by authors working in countries out of North America (Figure 5).

Discussion

The number of articles that measured alpha diversity in two leading ecological journals has increased through time, with a higher rate of increase after 1991. This fact may suggest a changing biopolitical landscape in the late 80s and early 90s that influenced scientific interests. Events like the National Forum on Biodiversity, the Convention on Biological Diversity, and others have stated clear research priorities on biodiversity studies, such as the importance of local inventories. The emergence of conservation biology as a discipline has also highlighted the need of a comprehensive knowledge on biological diversity prior to setting proper ways of using and preserving it. The breakpoint stated here for this change (1991) is arbitrary, but the findings can be taken as a starting hypothesis to assess how biological conservation and biopolitical aspects are influencing the academic job related to biodiversity.

The three types of methods used to measure alpha diversity (species richness, diversity indices and richness estimators) had positive relationships with time. By far, the most popular measure of alpha diversity was species richness. However, since 1994 there appeared to be an increase in the use of species richness estimation procedures. This was probably promoted by Colwell and Coddington's (1994) review about methods for estimation of species richness, and to the free access software provided by Colwell (2005, available since 1997). These sources encourage the use of a variety of non-parametric estimators such as the indices of Chao (1984, 1987).

In general, more studies were done with animals than with plants during this period of time. This finding is similar to what Stiling (1994) found. He evaluated 3108 articles published by three ecological journals (*Ecology*, *Oecologia* and *Oikos*) from 1987 to 1991, and found that animals were the organisms more commonly studied. However, when we divided animals into vertebrates and

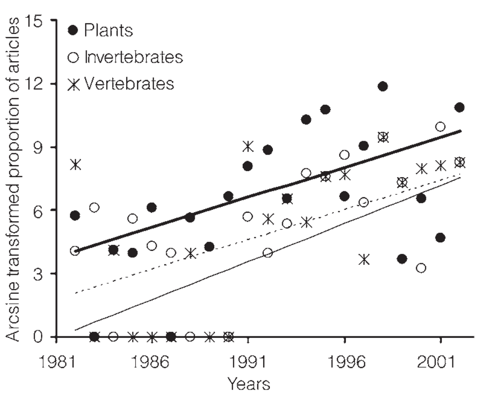

Figure 3. Proportion of articles (arcsine transformed) that focused on the main biological groups out of the total number of articles per year published in *Ecology* and *Ecological Monographs*, as a function of time. There are significant linear regressions of plants (bold solid line, r^2=0.62, N=21, d.f.=20, P<0.001) vertebrates (thin solid line, r^2=0.53, N=21, d.f.=20, P<0.001) and invertebrates (dashed line, r^2=0.53, N=21, d.f.=20, P<0.001).

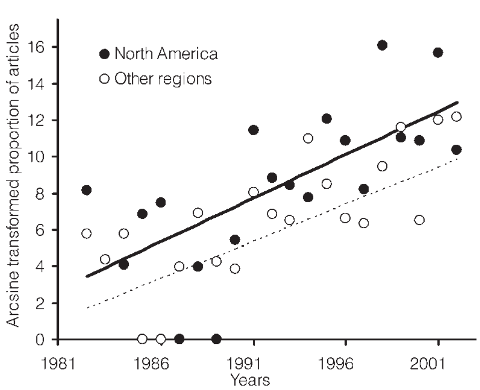

Figure 4. Proportion of articles (arcsine transformed) done in North America (solid line, r^2=0.58, N=21, d.f.=20, P<0.001) and other regions (dashed line, r^2=0.61, N=21, d.f.=20, P<0.001) out of the total number of articles per year published in *Ecology* and *Ecological Monographs*, as a function of time.

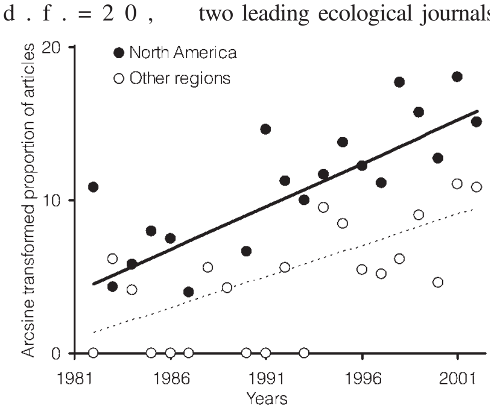

Figure 5. Arcsine transformed proportion of articles written by authors with adscription in North America (solid line, r^2=0.70, N=21, d.f.=20, P<0.001) and authors working in other regions (dashed line, r^2=0.49, N=21, d.f.=20, P<0.001) out of the total number of articles per year published in *Ecology* and *Ecological Monographs*, as a function of time.

invertebrates in our data base, each of these two groups had a lower number of articles than plants. In contrast, vertebrates are by far more frequently studied than plants in conservation biology papers (Fazey *et al.*, 2005a). In the present data set, the rates of increase in the studies done with plants, vertebrates and invertebrates were not significantly different. Each biological group has been studied differently, mainly due to fact that sampling and collecting methods differ, and that the determination of species in some groups, like fungi and prokaryotes, is difficult (Stiling, 1994).

More studies were done in North America, and their number increased at a higher rate than the number of studies done in other regions. This may be related to the fact that most authors worked in North America and that the journals reviewed herein are published in the United States. The place in which a journal is published may affect the number of studies done in a particular geographic region and the author's adscription. However, the same bias towards authors from and studies carried out in the United States was found by Fazey *et al.* (2005b) when they analyzed the papers published in three top conservation biology journals, one from United States and two from Europe. Obviously, doing research in other regions is more expensive and requires more effort than working in study areas near to the institution of adscription. For authors with a maternal language different than English, the requisite to write in this language may be an additional constraint for publication.

In conclusion, the analysis performed showed that in recent years studies on alpha diversity have gained importance in ecology, maybe as a result of the biodiversity crisis and the research priorities stated by conservation biologists. Of course, the trends reported in this paper are restricted to only two ecological journals, and further effort is needed to get a broader view in regards to the study on alpha diversity as a whole. Ecologists have not used unique methodological approaches, and continue using different methods. Among these methods, species richness is still the most popular measure of alpha diversity. However, in the last decade the rate of use of richness estimators has increased. This suggests that we are not only attempting to measure local diversity usually with incomplete inventories, but going further by predicting the unknown biodiversity that can be estimated out of the samples, although the use of richness estimators is not yet generalized in biodiversity studies. In order to get proper global perspectives on matters of biodiversity and conservation, journals devoted to publish research on ecological diversity should open their scope to include all life-forms and geographical regions.

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