

**Exactness and reliability
of nonparametric estimators of species richness
compared by simulation and field data**

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1 Introduction

1.1 *Theoretical background*

Since “The Theory of Island Biogeography” appeared (MAC ARTHUR & WILSON 1967) the number of species per area has gained new significance in ecological theory. It was then established that the number of species on islands decreases as the island area decreases. This theory initiated a fruitful discussion about the reasons for this species-area relationship. When island is referred to it is not necessarily meant literally. Equally, small habitat patches in a matrix can be islands for specialist species. As pointed out by BEGON ET AL. (1990) “... , there can be few natural communities lacking at least some element of islandness”.

For the species-area relationship three explanations are common (MAC ARTHUR & WILSON 1967). The first is, that a larger island offers a wider variety of habitats and therefore suitable conditions for more species. The second focuses on the level of balance between colonization and extinction. The third takes a more evolutionary point of view on the relationship between endemism and the balance between colonization and extinction.

Studies aiming to validate or disprove such explanations assume almost complete inventories of species groups. This can be presumed for species groups which can be detected relatively easily like plants or breeding birds for example, on islands which aren't too large. However, it is difficult to keep this assumption when studied species groups have a cryptic way of living. The situation becomes even more complicated on mainland islands with their weak habitat borders. Inevitably, the species list resulting from an inventory becomes a sample of the whole species richness. When taking samples of species communities, the effect of the catching effort and differently heterogeneous habitat structures cannot be eliminated from the species-area relationship (BALTANÁS 1992, WALTHER ET AL. 1995). In order to minimize this uncertainty when comparing species numbers from islands varying in size, the only way is to use accurate estimates instead of counts. Therefore, accurate estimates should be useful in the basic ecological field of species turnover in the context of the equilibrium theory (MAC ARTHUR & WILSON 1967).

BEGON ET AL. (1990) pointed out that “One way to characterize a community is simply to count or list the species that are present. This sounds a straightforward procedure that enables us to describe and compare communities by their species richness. In practice, though, it is often surprisingly difficult, partly because of taxonomic problems, but also because only a sub-sample of the organisms in an area can usually be counted”. Since species richness is a fundamental measure of biological diversity, this citation (BEGON ET AL. 1990) illustrates the importance of searching for methods to estimate species richness. Knowledge about the actual number of species in a given area is of crucial concern in scientific community ecology and is also highly important when dealing with conservation and management of

biodiversity (COLWELL & CODDINGTON 1994, BOULINIER ET AL. 1998). Species richness as such is frequently used as a variable reflecting sustainability when investigating the effects of human impact on biodiversity. This task calls for methods to compare species communities (CHAO ET AL. 2000) and to estimate rates of local extinction, turnover, and colonization, the variables being responsible for the changes of species richness of communities over time (NICHOLS ET AL. 1998B).

1.2 *Estimation of species richness*

Population ecologists have placed strong emphasis on the development of methods to estimate population parameters incorporating unknown detection probabilities of individuals. In contrast, community ecology has not seen a parallel development of methods that recognize and explicitly incorporate species recording probabilities. Accepting that usually no sampling effort is high enough to detect all species, a number of probabilistic estimators of species richness have recently been proposed, that were originally developed for population size estimation (BURNHAM & OVERTON 1979, CHAO 1987, COLWELL & CODDINGTON 1994, LEE & CHAO 1994, NICHOLS & CONROY 1996, BOULINIER ET AL. 1998, CHAZDON ET AL. 1998). The concepts of estimating local species richness by sampling can be divided into three groups: extrapolating species accumulation curves, fitting parametric models of relative abundance, and nonparametric methods (COLWELL & CODDINGTON 1994). All these methods have to cope with the statistical problem that assuming equal recording probability for the species within a community is definitely not justified (COLWELL & CODDINGTON 1994, BOULINIER ET AL. 1998). Moreover, BOULINIER ET AL. (1998) exemplarily showed by means of bird community data that the recording probabilities of sequences in samples vary.

The number of recorded species is clearly a function of the effort to detect them. Plotting the cumulative number of species discovered against any measure of effort, like number of samples, trap-days, or hours of observation, the species accumulation curve appears. The shape of this curve is affected by the order of adding the samples. To avoid this, there are two ways of randomizing the samples (COLWELL & CODDINGTON 1994), computing a rarefaction curve (sampling without replacement) (HECK ET AL. 1975) or a random placement curve (COLEMAN 1981). Fitting these curves to asymptotic or non-asymptotic functions makes it possible to extrapolate them and to estimate the "true" species richness. Numerous functions and methods to fit them have been used (PALMER 1990, BALTANÁS 1992, SOBERÓN & LLORENTE 1993, COLWELL & CODDINGTON 1994). The most famous is the two-parameter hyperbola also known as Michaelis-Menten or Clench equation (CLENCH 1979, RAAIJMAKERS 1987, KEATING & QUINN 1998).

A different approach to species richness estimation is fitting parametric models directly on patterns of relative abundances as expressed in frequency distributions of species abundances. The most promising distributions (COLWELL & CODDINGTON 1994) are probably the lognormal, Poisson-lognormal, log-series, and the zero truncated generalized inverse Gaussian-Poisson.

There are parametric and nonparametric approaches to the Bayesian concept of estimating species

richness (MIGNOTI & MEEDEEN 1992, SOLOW 1994). The common concept is to find the prior value of a parameter, the number of species observed in samples for example, and to use a probabilistic model to derive estimators, that estimate the number of unseen species from the additional species of additional samples. The complicated calculations necessary for these methods and a lack of available computer programs probably contributed to the fact that the Bayesian approach has rarely been used.

The concept of the nonparametric abundance-based estimators of species richness is to use the number of species present in a single sample with exactly one individual (singleton), two individuals (doubletons), and so on. Assuming that this distribution of the numbers of individuals per species is known and is equal in all species communities, the number of species which were not recorded can be estimated. The moment estimator (CHAO 1984), which is based on singletons and doubletons, has been used frequently, maybe because of its simplicity. The jackknife procedure is also used to estimate species richness from empirical species abundance distribution data. It is programmed in SPECRICH (HINES 1996, HINES ET AL. 1999) and is based on a limiting form of the jackknife estimators (BURNHAM & OVERTON 1979), which can be used when no information on the number of recording occasions is available but the number of individuals was detected for each species. However, this abundance-based version of the jackknife does not seem to be in use. Recently, an abundance-based coverage estimator (ACE) was introduced (CHAZDON ET AL. 1998). This is derived from coverage estimators of the numbers of classes (CHAO & LEE 1992, CHAO ET AL. 1993) and is programmed in EstimatS (COLWELL 1997).

Nonparametric incidence-based estimators use presence/absence data (records) of species of a series of spatial or temporal samples without accounting for the number of detected individuals. This setup is statistically similar to mark-recapture methods, however, with species being the units sampled. Thus some of the methods are useful and used for both tasks (BURNHAM & OVERTON 1979), estimating the abundance of single species and estimating the species richness of communities. As stated above, the recording probability of species is different and the general recording probabilities of samples, whether they be spatial or temporal, are mostly different. Thus, to estimate species richness, only those methods are useful, which in terms of abundance estimation can incorporate individual heterogeneity (h), denoted as model M_h , or additionally temporal heterogeneity (t), denoted as model M_{th} (CHAO 2001).

The bootstrap method of species richness estimation uses a procedure of random sampling with replacement to estimate the bias of the number of recorded species compared to the unknown "true" number of species (SMITH & VAN BELLE 1984). It must be noted that this bootstrap estimator of the bias has a maximum value, which is defined by the number of samples and which has no biological meaning. This estimator of species richness has been rarely used.

The moment estimator of CHAO (1987) is very easy to calculate. The estimated number of species is the number of recorded species corrected by the relation of the numbers of species recorded once (f_1) and twice (f_2), which is probably the reason for its frequent use.

A number of martingale estimators have been proposed for species richness estimation (CHAO ET AL. 1996), however, they are not widely used. A special case of them is exactly equal to one of the coverage estimators (CHAO & LEE 1992).

BURNHAM & OVERTON (1979) were the first to propose the application of the jackknife procedure to species richness estimation from a series of sampling quadrats. Later on, the first order jackknife (HELTSHE & FORRESTER 1983) and the second order jackknife (SMITH & VAN BELLE 1984) were suggested independently for species richness estimation. The jackknife method derives the number of unseen species from the numbers of species lost when removing single quadrats from the sample. Actually, the jackknife estimators are the most frequently used nonparametric species richness estimators. They are easily available in computer programs like CAPTURE (REXSTAD & BURNHAM 1991), SPECRICH2 (HINES 1996), and EstimatS (COLWELL 1997).

In estimators using the concept of coverage, the parameter of interest is not estimated directly but by estimating the coverage of the samples relative to the "true" value. This was first proposed by CHAO AND LEE (1992) for population size estimation in the case of heterogeneous capture probabilities of individuals as an alternative estimator for the jackknife (REXSTAD & BURNHAM 1991). COLWELL & CODDINGTON (1994) first used some of these coverage-based estimators for estimating species richness. A modified version (LEE & CHAO 1994) was introduced as an incidence-based coverage estimator (ICE) by CHAZDON ET AL. (1998). Some of these estimators are available in EstimatS (COLWELL 1997) and CARE2 (CHAO & YANG 2003).

1.3 Comparison of species richness estimators

Since BUNGE & FITZPATRICK (1993) pointed out the lack of studies comparing the methods of estimating species richness, some work has been done in this area. However, these studies always compared more or less small numbers of selected species richness estimators (e.g. PALMER 1990, COLWELL & CODDINGTON 1994, WALTHER & MORAND 1998). Thus it is difficult to get an overview, which of these estimators compete well. Moreover, "true" species numbers which can be compared with the estimates are never known from field inventories. Therefore, in these studies the performance of the estimators was evaluated by comparing the estimates with educated guesses of "true" species numbers. PALMER 1991, BUNGE & FITZPATRICK 1993, and COLWELL & CODDINGTON 1994 regarded some of the nonparametric estimators as the most promising. According to them, the performance of these estimators is discussed first.

In several studies, the jackknife estimators, especially, the first order and the second order jackknife, showed to perform quite well (e.g. PALMER 1990, PALMER 1991, BOULINIER ET AL. 1998, CHAZDON ET AL. 1998). They are likely to occur in all studies comparing species richness estimators, therefore, they turned out to be a kind of reference. The first attempt to use coverage estimators for species richness estimation showed little success (COLWELL & CODDINGTON 1994). An enhanced version (LEE & CHAO 1994)

was introduced as an incidence-based coverage estimator (ICE) and showed satisfying performance (CHAZDON ET AL. 1998). In a simulation the martingale estimators (CHAO ET AL. 1996) did not perform better than one of its special cases, the coverage estimator of CHAO & LEE (1992). Nevertheless, these two concepts are the only ones which seem to offer comparable or even more accurate and reliable results than the jackknife approach (BUNGE & FITZPATRICK 1993).

The moment estimator showed little bias (COLWELL & CODDINGTON 1994, WALTHER & MORAND 1998, CHAZDON ET AL. 1998), however, it lacked accuracy and reliability (CHAO 1987). Furthermore, it follows from the formula of this estimator that it fails, if f_2 is zero. Not all nonparametric estimators performed well. The bootstrap method was not very successful in estimating species richness, because it clearly underestimated the true species number (COLWELL & CODDINGTON 1994, CHAZDON ET AL. 1998, HERZOG ET AL. 2001).

Another class of estimators, the abundance-based nonparametric species richness estimators, generally could not reach the accuracy and reliability of the incidence-based ones (COLWELL & CODDINGTON 1994, WALTHER & MORAND 1998). The abundance-based jackknife estimator does not even seem to be in use. The abundance-based coverage estimator (ACE) did not perform satisfactorily (CHAZDON ET AL. 1998).

Estimating species richness by fitting accumulation curves is common practice. Nevertheless, these methods usually did not reach the accuracy and robustness of the nonparametric competitors (BUNGE & FITZPATRICK 1993, COLWELL & CODDINGTON 1994). Only fitting the accumulation curve to the Michaelis-Menten equation partly resulted in comparably good results. Different equations proved to fit the accumulation curve properly for different species communities. However, there is no rule for choosing the most appropriate one until most of the species are seen. Estimators based on fitting parametric models directly to patterns of relative species abundances usually showed a clearly worse performance than the nonparametric estimators (PALMER 1990) or at best performed similarly (BALANÁS 1992). The basic problem again is finding the correct model for an individual species community without already knowing almost everything about it.

Even if elaborate computations have recently become more affordable, the only comparison of the performance of Bayes estimators of species richness to that of the other approaches can be found in MINGOTI & MEEDEN (1992). In this case the Bayesian approach seemed to achieve comparably good results as the first order jackknife.

Considering the brief discussion of methods estimating species richness above led to the decision to focus this study on nonparametric estimators, which are based on discrete-time mark-recapture-like samples. The chosen estimators are shown in more detail in Chapter 5 and the Appendix.

As the case for every estimation, species richness estimation needs an estimation of a corresponding measure of error. For each of the species richness estimators the authors developed a corresponding estimator of the standard error. However, the results of these estimators of the standard error are

not comparable between the estimates of species richness. Generally, the bootstrap and the jackknife method showed to be useful for estimating the standard error of any estimation (MILLER 1974, MANLY 1977, EFRON 1981). For species richness estimators the bootstrap was recommended (CHAO ET AL. 1996, NICHOLS ET AL. 1998B, CHAO ET AL. 2001), however, neither the bootstrap nor jackknife method were evaluated for species richness estimation and they have rarely been used for this task.

Different groups of species richness estimators were evaluated by simulations as well as with field data. Whereas field data cannot provide the "true" species number, simulated communities of species are in danger of not reflecting real patterns. However, they have the advantage that their "true" number of species is known. Some of the nonparametric estimators shown above were tested with the beta distribution modeling the distribution of the recording frequencies for heterogeneous capture probabilities (BURNHAM & OVERTON 1979, CHAO 1987). As very little is known about the recording probabilities of species in the field, every theoretical distribution is in danger not to reflect the conditions of real species communities. Therefore, it is necessary to have an excellent field data base, like in this study, to derive distributions of recording frequencies which accurately reflect those of real communities.

Generally, factors like effort and heterogeneity of sampling sites and periods can be assumed to affect the accuracy and reliability of species richness estimates. On the one hand, little is known about how factors like effort or heterogeneity of sampling sites and periods affect the distribution of recording probabilities and consequently the accuracy and reliability of the estimates. On the other hand, the reasons for the differences in the performance of estimators of species richness in several studies based on field data as well as simulations are poorly understood. Thus, it is likely that an improved knowledge of the factors affecting the recording probabilities of species will be an improved basis for studying the usefulness of selected estimators for species richness estimation.

The object of this study is to identify and model the factors, which modify the basic probabilities of species being recorded in samples and their effect on estimates of species richness as well as on the associated estimates of standard errors. This leads to three hypotheses:

- The distribution of species' recording frequencies is a result of the real abundance of species, the recording effort, and different sources of heterogeneity superimposing on each other.
- The species group, the recording effort, and sources of heterogeneity in samples can be used to indicate which of the species richness estimators will work best.
- Bootstrap and Jackknife estimators of standard error are useful for species richness estimates.

1.4 Integration in the RIVA project

This study was part of a project named “Development of a Generalized Robust Indication System for Ecological Change in Riverine Wetlands” (“Übertragung und Weiterentwicklung eines Robusten Indikationssystems für ökologische Veränderungen in Auen”), in short, RIVA (funded by the German Federal Ministry for Education and Scientific Research). This project aimed to develop an indicator system to monitor and to predict changes in species communities depending on changes in the intensity and frequency of floods in riverine wetlands (SCHOLZ ET AL. 2001). Investigating methods for species richness estimation was part of developing a tool to study the robustness of the indication system against reduced effort.

As it is very elaborate to get high quality data sets on species richness, it is necessary to cooperate with botanical and zoological specialists in a research project, when trying to work on species richness estimation. This particularly applies to data which is suitable for analyzing species richness estimators which require capture histories like those from mark-recapture studies for estimating population size. Therefore, this study was incorporated within the RIVA project using its study areas and sampling design.

My task in RIVA was to develop a tool for investigating the robustness of the zoological indication system against a reduced sampling effort (Fig. 1). Assuming, that the most important factor for a correct indication result

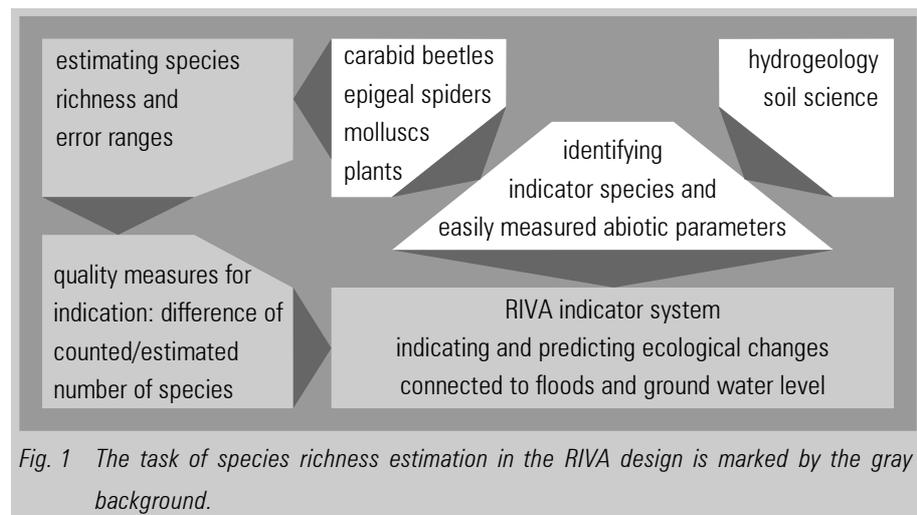


Fig. 1 The task of species richness estimation in the RIVA design is marked by the gray background.

is having captured most of the species of an area, then an estimation of the species number would be a tool to measure the quality of an indication result. In particular, the difference between the counted and the estimated number of species of a community used for indication, turned out to be a measure for the accuracy and reliability of an indication (FOLLNER 2005).

1.5 Structure of the thesis

This thesis is written as a series of future papers surrounded by an introduction, methods and a discussion. Chapter 3 is the first of the foreseen papers. Therein it is shown on the basis of field data, how sampling effort, sampling design, characteristics of species groups, and different sources of het-

erogeneity affect the curve shape of the distribution of species' recording frequencies. These recording frequencies are the basic data of species richness estimates from mark-recapture methods. However, the factors affecting them cannot be studied separately from field data. In Chapter 4 the results of a simulation are presented, which show how single factors, sampling effort for example, do affect the distribution of species' recording frequencies.

As the "true" number of species is never known from field data, the rating of species richness estimators can only be done by a simulation reflecting the factors, which affect their accuracy and reliability. The aim of Chapter 5 is to show which of the species richness estimators of this study is the most useful under which conditions. Moreover, guidelines are given to choose the best estimator for a certain data set on the basis of the number of species records and the distribution of species' recording frequencies. In Chapter 6, the associated estimators of the standard error of the estimates are compared with two alternative methods, the bootstrap and the jackknife.

The last of these foreseen papers (Chapter 7) applies the species richness estimators to the data collected in the RIVA-project with their differences in the factors sampling effort, sampling design, characteristics of species groups, and different sources of heterogeneity of samples. These examples show that the species richness estimators indicate equal patterns of relative performance in terms of the number of species records and the curve shape of the distribution of species' recording frequencies in the field data and in the simulation.

2 Study area and general methods

2.1 Study sites and sampling design

The RIVA project was carried out at three study areas along the river Elbe in Germany. These were situated in the grassland of the floodplains of this river. The data for this thesis all originate from the main study area of RIVA called Schöneberger Wiesen, which is situated in Saxony-Anhalt and belongs to the Middle Elbe Biosphere Reserve (Fig. 2).

In the main study area, 36 study sites were selected by stratified random placement (Fig. 3). This was the best solution compromising the assumptions of multivariate statistics and the achievable effort. It was assumed that the distribution of species in riverine wetlands is ruled by parameters, which are connected to flooding. Therefore, the study area was stratified by geomorphological parameters into three groups, which could be assumed to have different probabilities of being flooded. Inside each of these strata, the study sites were placed by randomly selecting the coordinates of points from a grid in the study area as the first corner of a study site. These points were located in the study area using a global positioning system. Then, the study sites each about 450 m² in size (Fig. 3) were placed in the direction which promised least heterogeneity inside.

All hydrological and pedological (abiotic) as well as zoological and botanical (biotic) surveys were investigated at each study site. To avoid disturbance, it was necessary to organize the work of the different scientists. Thus, each of the sciences had its fixed positions in the scheme of the study site as shown for zoology and botany (Fig. 3).

As expected, the results of the RIVA project confirmed that mainly parameters of water-level, such as the duration of flooding and the distance of groundwater levels to the surface, affect the species' spatial distribution in riverine wetlands (HILDEBRAND ET AL. 2005). The curve of water and groundwater levels respectively of an exemplary study site (Fig. 4) shows that during the two years of sampling very low and very high water and groundwater levels respectively appeared (BÖHNKE & FOLLNER 2002). On the other hand, the duration of dry and flooded periods was quite normal. This was true for a number of low-lying study sites but not for those on higher terrain. Because of the two quite high flood peaks during the winter of 1998/1999 (Fig. 4), these were flooded for an unusually long period. Nevertheless,



Fig. 2 Location of the study area.

this are normal hydrological dynamics in floodplains and therefore it can be assumed that the species communities studied are typical.

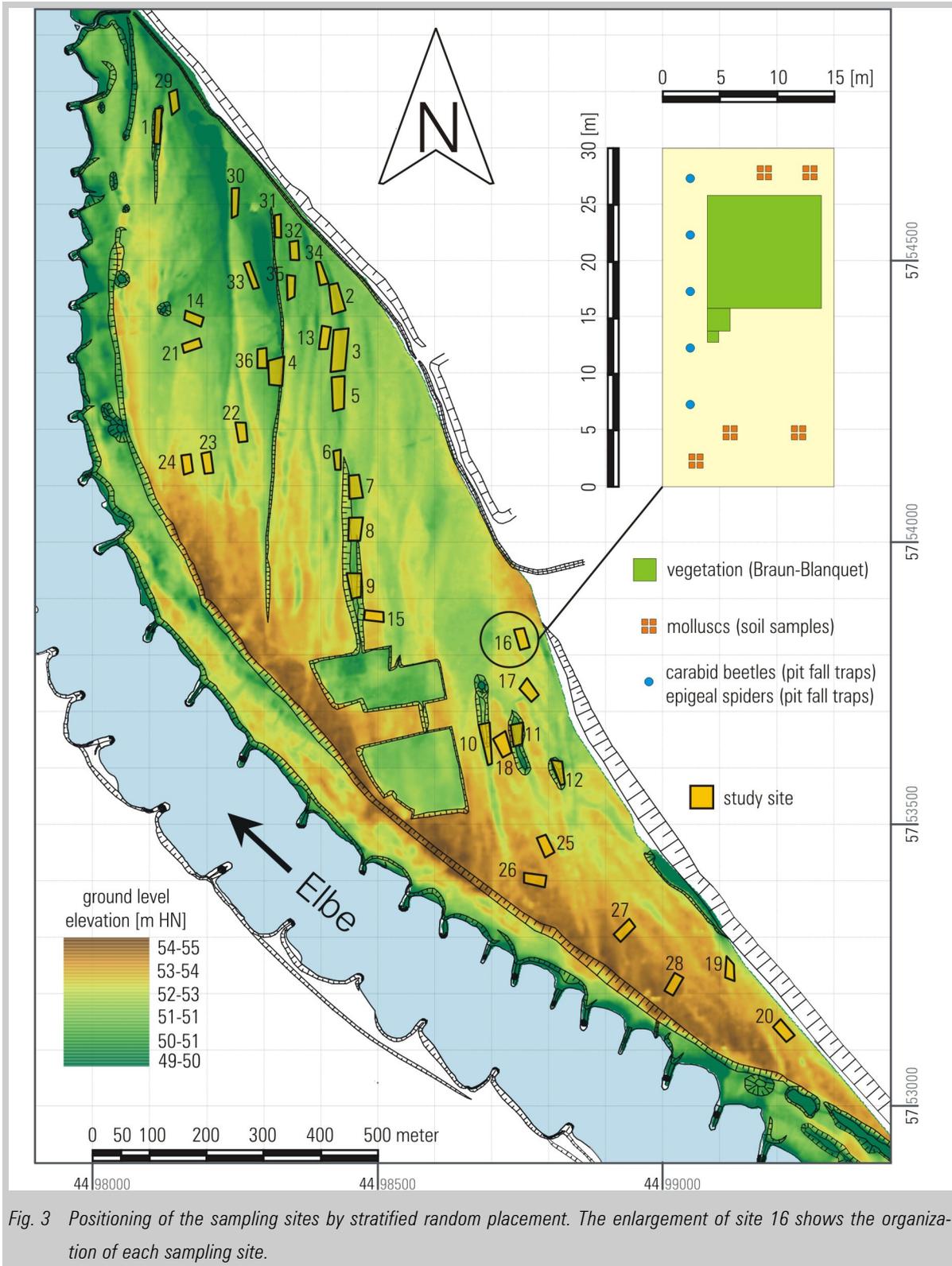


Fig. 3 Positioning of the sampling sites by stratified random placement. The enlargement of site 16 shows the organization of each sampling site.

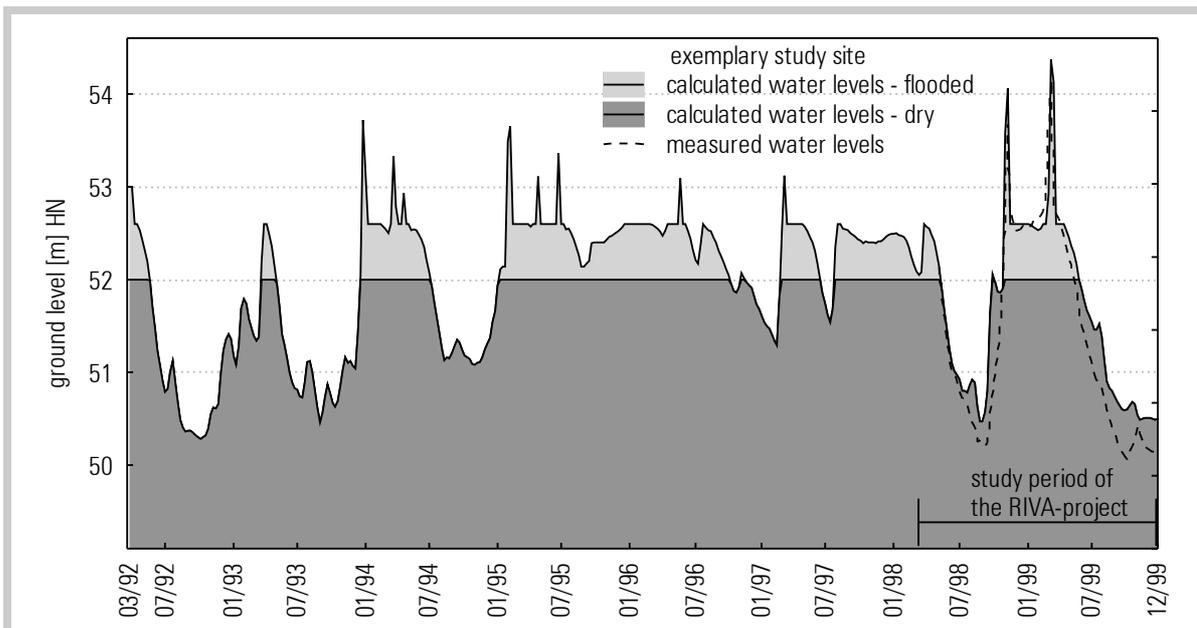


Fig. 4 Water level changes on an exemplary study site. For details of the calculation see BÖHNKE & FOLLNER (2002).

All the dynamic hydrological parameters, in particular the duration of flooding per year and the mean depth of groundwater during the vegetation period showed a quite similar spatial distribution in the study area (FOECKLER ET AL. 2005). Therefore, these parameters affected the spatial distribution of the species in a similar way. The effective cation exchange capacity of the first 20 cm of soil, however, is much less dynamic and its spatial distribution is quite different. As a soil parameter, it affects mainly the species distribution of plants (RINK & HETTRICH 2005). The knowledge of the distribution of these parameters was necessary to combine homogeneous groups of study sites for studying the distributions of species' recording frequencies and the performance of mark-recapture methods for species richness estimation

2.2 Species groups and recording methods

The species groups used in this study, namely, carabid beetles, molluscs, plants, were chosen to support the aims of RIVA. Epigeal spiders were studied additionally. The concept was to take groups of different mobility because it was not known which range of mobility species may have that is useful for indicating important parameters in riverine wetlands. According to the spatial scale of riverine wetlands, carabid beetles are quite mobile, molluscs much less and plants are of course immobile. These differences in mobility make these species groups useful for comparing distributions of recording frequencies and species richness estimation.

The methods used to record the species of the different groups were very different, last but not least because of their difference in mobility. Thus, the epigeal spiders were added because they were trapped with the same traps as the carabid beetles. These two species groups can therefore be com-

pared directly as the captures originate from the same traps during the same periods and thus are affected by the same spatial and temporal heterogeneity of samples. The species identification was carried out by the specialists working in RIVA (i.e. for carabid beetles, molluscs, and plants) or by an external specialist (in the case of epigeal spiders). As the names of the species do not matter in the context of this study, the nomenclature used for identification will not be cited.

Carabid beetles and epigeal spiders were caught by pitfall trapping (BARBER 1931, TRAUTNER 1992). At each study site, five plastic cups were placed in a line five meters apart (Fig. 3), which is a common trapping design (TRAUTNER 1992). The six sampling periods for carabid beetles in the RIVA-project lasted four weeks, with a standard interval for emptying the pitfall traps of two weeks. To obtain mark-recapture-like data of closed species communities in a common temporal way, eight consecutive two-day periods were integrated into three of the sampling periods. In these short time periods carabid beetles and epigeal spiders were caught and the trapped animals conserved in a 7% solution of acetic acid.

Taking soil samples is the standard method for studying species communities of terrestrial molluscs (OGGIER ET AL. 1998). A quarter of a square meter is a frequently used size (COLLING 1992), which was realized by taking five soil samples of 0.05 m² per study site. The placement of the sampling points was the same on each study site (Fig. 3). As the change in mollusc communities is usually slow and the species can easily be seen over the whole year, two sampling periods per year are biologically sufficient. However, as soil samples are quite destructive, they were taken quite close to one another (Fig. 3). Small mollusc species can only be obtained by sieving the soil samples. Sieving was done by hand for the first sampling period and mechanically for the three remaining ones. The results in terms of numbers of recorded species and individuals was so different (DEICHNER ET AL. 2003) that the results of the first period cannot be compared to the subsequent results which were therefore the only ones used.

At first it was not planned to include plants in the study on species richness estimation. Thus, the sampling design on the single study sites was not optimized in order to enable species richness estimation with mark-recapture methods on each single study site. Sampling plots of three different sizes 1 m², 4 m², and 100 m² (Fig. 3) were used to study the vegetation with standard methods (BRAUN-BLANQUET 1964) and to compare the results with three levels of effort. Because of the changing visibility of plant species during the growing season there were six sampling periods.

3 Distributions of species' recording frequencies in field data

3.1 Introduction

The basic concept of this study is to find those estimators of population size which are most useful for estimating species richness. The simplest of the methods used to estimate population size assumes that all specimens of a population have an equal probability of being captured (OTIS ET AL. 1978). However, it is obviously wrong to assume that all the species of a community have an equal probability of being recorded (COLWELL & CODDINGTON 1994, BOULINIER ET AL. 1998, NICHOLS ET AL. 1998A).

The most important data set for the estimation of the number of individuals of a species' population is a condensed capture history, the distribution of the species' capture frequencies. The capture frequencies are not a direct reflection of the capture probabilities of the individuals but of the probabilities of an individual being captured once (f_1), twice (f_2), and so on. If the capture probabilities are equal, the curve shapes of the distributions of capture frequencies are always unimodal (Fig. 5).

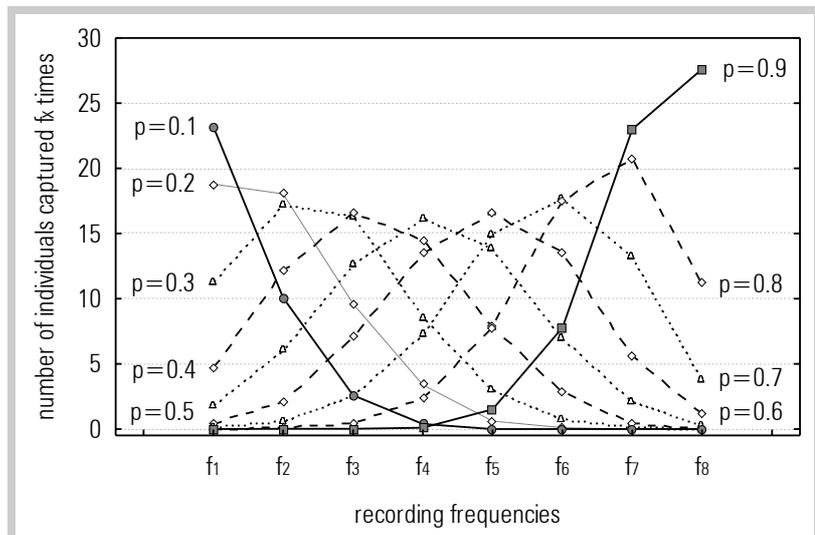


Fig. 5 Distributions of capture frequencies f_i based on a simulation with equal capture probabilities (p) of different height (population size: 60, number of samples: 8).

However, CODDINGTON ET AL. (1996) reported from their inventory on spiders that the distributions of species' recording frequencies are slightly bimodal. Thus, one consequence of unequal species' recording probabilities seems to be that the distributions of the recording frequencies can be bimodal. The nonparametric estimators of species richness are based on this distribution or on parts of it. As these distributions seem to reflect the dissimilarity to equal recording probabilities and affects the performance of the estimators, the set of curve shapes based on equal probability (Fig. 5) should be kept in mind when studying the curve shapes of recording frequency distributions of species communities from the field.

Several factors contribute to an unequal detectability of species. The differences in the recording probabilities of species originate on the one hand from their basic catchability, which is affected by factors like mobility and trapping method, and on the other hand by their different population sizes.

Hence, a species with a small recording probability from the specimens, nevertheless, can be trapped regularly because of its high population size, and the other way round. In normal recording efforts, this usually leads to a wide range of species' recording probabilities and, hence, a bimodal distribution of the recording frequencies (FOLLNER & HENLE 2001). Species inventories were often done in a variety of habitats (CODDINGTON ET AL. 1996, LONGINO ET AL. 2002). Such samples used for species richness estimation are more or less heterogeneous. In most cases little is known about this heterogeneity and, consequently, its effect on the distributions of the species recording frequencies and on the accuracy of species richness estimates is unclear.

Basically, the beta distribution is able to model unimodal and bimodal distributions, which is probably the reason for applying it to simulations aiming to test the performance of estimators of population size in the case of heterogeneous capture probabilities (CHAO 1987, BURNHAM & OVERTON 1979). However, BURNHAM & OVERTON (1979) used parameters for this distribution, which did not result in bimodal distributions, probably however, because they tested the jackknife as a population size estimator. The few simulations which are done with estimators of species richness did not account for the curve shapes of the distributions of species' recording frequencies found in field data. Thus, there is obviously a lack of knowledge about the variation of curve shapes which this distribution can have in field data, and about the factors which create this variation.

The curve shape of the distribution of the species' recording frequencies can be assumed to be one main parameter affecting the accuracy and reliability of methods to estimate species richness. Thus, in order to get realistic simulation scenarios used for studying the performance of estimators it is important to know which factors drive these parameters. The aim of this chapter is to study by means of field examples how factors like sampling effort, characteristics of the species group or heterogeneity of study sites and periods affect the distributions of species recording frequencies.

3.2 *Methods and data*

This study has been the concerted effort from the joint project RIVA. The biotic data and, in terms of ecological interpretation of spatial and temporal heterogeneity, also the abiotic data originate from the concerted field work of the participants (Fig. 3). The data were collected on a grassland study area, in the floodplains of the river Elbe in Saxony-Anhalt in Germany (Fig. 2), an area which belongs to the Middle Elbe Biosphere Reserve. For details of the study area see Chapter 2.

The statistical tests, Spearman Rank Correlation and χ^2 tests, were done with the commercial statistic software STATISTICA (STATSOFT 2001).

3.2.1 *Species groups and trapping methods*

The species groups used in this study are carabid beetles, epigeal spiders, molluscs, and plants.

Groups with different mobility were chosen to study the effects of mobility on catchability and, hence, on the distributions of the species' recording frequencies.

In order to get the species records, standard methods were used. Carabid beetles and epigeal spiders were caught by pitfall trapping (BARBER 1931, TRAUTNER 1992). The catches of carabid beetles and epigeal spiders originate from the same traps over the same periods and are therefore affected by the same spatial and temporal heterogeneity of samples. Therefore, these two species groups can be compared directly. The molluscs were recorded from soil samples (COLLING 1992). Five samples can be assumed to be the minimum number when applying "multisession" mark-recapture methods (OTIS ET AL. 1978). Thus, for epigeal spiders, carabid beetles and molluscs, five traps and soil samples respectively were taken per study site. This enables the species number per study site to be estimated. The plants were recorded (BRAUN-BLANQUET 1964) on plots of 1 m², 4 m², and 100 m² on each of the study sites, since it was not initially planned to use them for studying species richness estimation. Therefore, it is not possible to estimate the species numbers of single study sites for plants, nevertheless, it is possible to take several sites or periods to do this (see the following chapter). The identification of species was carried out by specialists within the joint project.

3.2.2 Study sites and study periods

Species richness estimation with "multisession" mark-recapture methods requires at least five samples (OTIS ET AL. 1978) of the estimated species community. The samples can originate from a number of sites (spatial samples) being sampled during one or more pooled periods, or from a number of periods (temporal samples) being sampled on one or more pooled sites. The sampling design of the RIVA-project provides data of species records, which enable both methods of sampling and pooling.

In the RIVA-project carabid beetles and plants were sampled over six periods (Fig. 6), molluscs over four periods. In order to get additional mark-recapture-like temporal samples of carabid beetles and epigeal spiders, three periods of short-term sampling were conducted (Fig. 6). This means that the pitfall traps were emptied for eight consecutive two-day periods. A period of 16 days is short enough to ensure that species communities are almost closed. This allows for getting a real temporal mark-recapture data set for estimating the species richness of these two species groups. Because of limited time and personal resources, 20 sites from the study area were selected for this short-term sampling.

		1998										1999									
		4	5	6	7	8	9	10	11	12	1	2	3	4	5	6	7	8	9	10	
concerted RIVA field periods	molluscs		■				■								■				■		
	carabid beetles		■		■		■								■		■		■		
	plants		■												■				■		
short time periods	carabid beetles				■		■														
	epigeal spiders				■		■										■				

Fig. 6 Concerted field periods of the RIVA-project (dark gray) and short time trapping periods (light gray).

This sampling design provides two different kinds of temporal data sets which can be used for species richness estimation. Carabid beetles and plants were recorded over the six concerted sampling periods of the RIVA-project (Fig. 6). Provided that the species communities of these species groups did not change too much and that the estimators can cope with the seasonal changes, the records can be used temporally to perform species richness estimations on a two-year scale. The short-term samples for the epigeal spiders and the carabid beetles (Fig. 6) provide temporal estimates of species richness with mark-recapture-like samples on a scale of approximately two weeks. Soil samples to record the molluscs were taken four times (Fig. 6) over two years. Thus, a species richness estimation of molluscs can only be carried out spatially.

The samples of carabid beetles, molluscs, and plants originate from 36 study sites of the concerted study area (Fig. 3). The samples of the epigeal spiders and the short-term samples of carabid beetles originate from 20 of them. These study sites provide spatial samples for estimating species richness. As the 36 study sites cover quite a large range of environmental factors, reasonably homogeneous spatial samples can only be achieved by finding ecologically-similar groups of study sites. Thus, it was crucial to know something about this spatial heterogeneity. Within the RIVA-project the differences in abiotic parameters of the study sites were investigated as well as their effect on the spatial distribution of species. The abiotic factors contributing to the composition of species communities in floodplain grasslands (RINK 2003) were identified, so it was known which study sites were similar in species composition and hence, ecological groups of similar study sites could be pooled.

3.2.3 *Spatial and temporal pooling of captures*

Samples used for estimating species richness can be either spatial or temporal. Usually, species inventories are conducted spatially which means that the species are recorded at a number of sites over a definite but normally not for the same period (HELTSHE & FORRESTER 1983). On the other hand the classical mark-recapture data are temporal, which means that individuals are recorded on one site over a number of consecutive periods (OTIS ET AL. 1978). To be able to compare these two sampling designs in their effect on the distribution of the species recording frequencies, the periods of short-term sampling were designed to obtain a data set, which could be used in both ways. From a statistical point of view, the spatial and temporal direction of the data is equivalent. However, the heterogeneity of sampling periods can differ from that of sampling sites. In this case, the distributions of the species' recording frequencies and the number of species records differ depending on the direction in which the data set is pooled.

The basic sample is a species list of one site of one period (Fig. 7). For the spatial way of pooling, the species lists of all periods are added up for every sampling site. For the temporal way of pooling, the species lists of all sites are added up for every sampling period. These combined species lists are

then the basic samples of the species' recording histories and, hence, of the distributions of species' recording frequencies (Fig. 7). This is the only way to interpret the effects of spatial versus temporal heterogeneity separately inside a data set used for species richness estimation.

The effect of different effort on the distributions of species' recording frequencies was studied by using subsamples of the data sets. The frequency distributions when using all five traps per site was compared to the distributions of mean frequencies for all possible permutations for four, three and two traps as well as with the mean from using single traps. The permutations were conducted by systematically using every possible combination of two, three and four of the species records originating from the traps from each site. The distribution of the mean frequencies when using four traps for

example consists of the mean values of the frequencies calculated from all combinations of four traps. Recording frequencies of species are in fact discrete values, thus the appropriate diagrams to visualize them should be histograms. On the other hand these discrete values are an image of the continuous probability of a species having a particular probability of being recorded. Thus, it is appropriate to visualize the distributions of species recording frequencies as quasi continuous line plots as done here.

3.3 Results

Three main factors proved to affect the curve shape of the distribution of species' recording frequencies in a complex way: sampling effort in the field, behavioral factors of the species groups according to habitat structure and weather and the extent of variability of the study sites and the study periods respectively. This resulted in a "family" of distributions of species' recording frequencies which can be unimodal with a maximum with small recording frequencies to bimodal with most of the species recorded either rarely or frequently. The curve shapes of this "family" of distribution clearly differed from those with a variety of equal recording probabilities (compare Fig. 5). Consequently, it could be

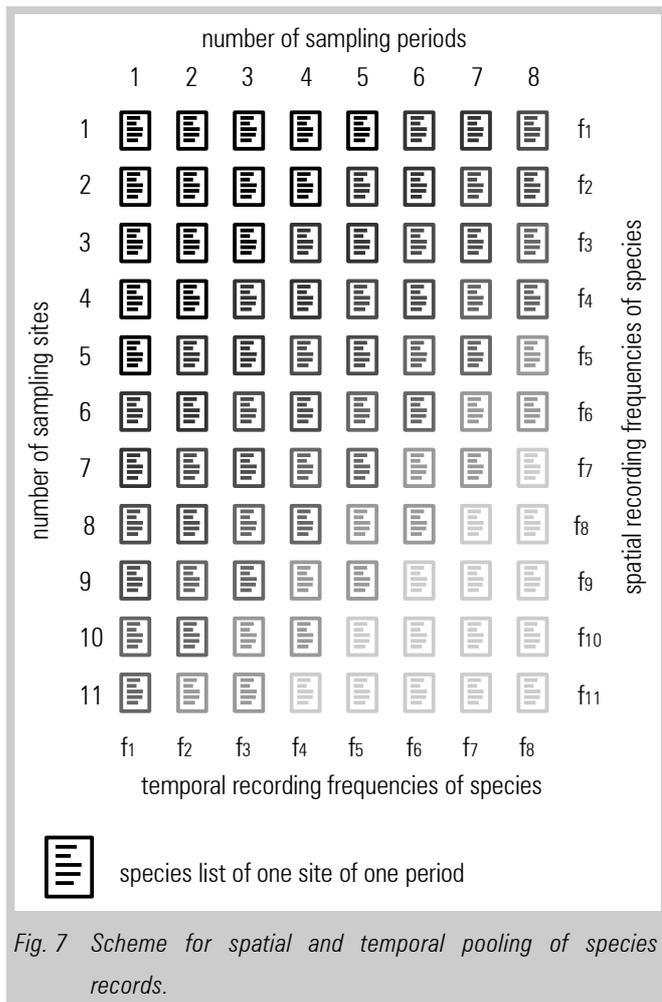


Fig. 7 Scheme for spatial and temporal pooling of species records.

concluded that the members of species communities always have a wide range of recording probabilities.

The sampling design of the RIVA-project provided a large number of potentially instructive combinations of species records (see Chapter 3.2). This made it possible to compare the effects of sampling effort, characteristics of species in their habitats, and sampling sites and periods respectively. From this variety of field data, instructive examples are chosen to show normal correlations between these factors and their effects on the curve shape of the distribution of species' recording frequencies as well as instructive exceptions.

3.3.1 Effect of short-term sampling on species records

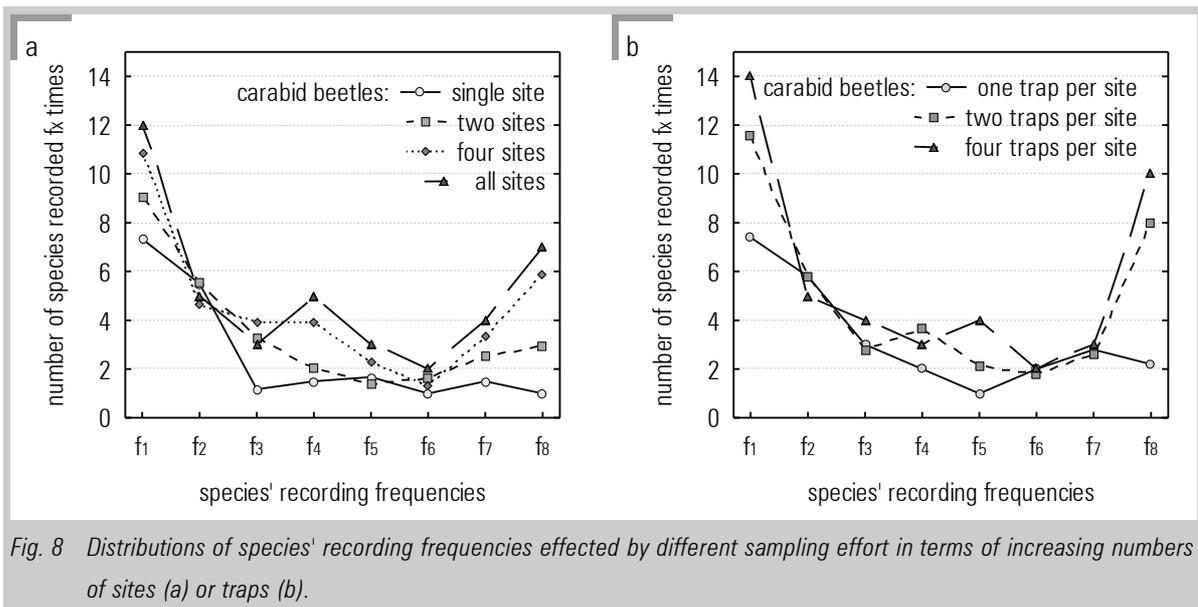
Over three periods, short-term sampling was performed by emptying the traps of carabid beetles on eight consecutive periods of two days (see Chapter 3.2.2) at 20 of the study sites, which were pooled to three groups of sites, namely, dry, medium dry, and moist. The data used to compare the trapping results, were the numbers of trapped individuals per day and species. Only those species were included, where more than one individual had been trapped over the period. It is expected to perceive the effect of the short-term sampling on the number of trapped individuals when comparing the mean trapping results per day from these 16 days to those from the following trapping period where traps were only emptied at the end of the period.

In three of the nine samples originating from the three site groups and the three sampling periods, fewer individuals were trapped per day over the short-term period compared to the undisturbed period. The difference between the numbers of individuals trapped over eight consecutive two-day short-term periods versus the undisturbed period was significant in only two cases (significance level $p = 0.05$, Wilcoxon test for paired samples with N between 10 and 39). Thus, there was no evidence that short-term sampling affects trapping success.

3.3.2 Recording effort

The example of the carabid beetles (Fig. 8) shows the general development of the distribution of species' recording frequencies, which became more bimodal with increasing effort. Examples of this kind could be found in all species groups. Other examples of species records from the field show exceptions, which were not rare and not mainly characteristics of the species group (compare the following chapter), but are shown in Chapter 3.3.4 to be correlated with differences in species recording probabilities between samples.

When using the records of periods as samples, the effort can be increased either by adding sites of a homogeneous group of sites or by using an increasing number of traps per site. Adding sites introduced heterogeneity in a different way to adding traps. In both cases the shape of the curve changed



in a characteristic way depending on the effort. The curves resulting from low effort, i.e. with single sites and single traps per site (Fig. 8) looked very similar to curves resulting from a small but equal recording probability of the species (Fig. 5). However, with increasing effort, i.e. more sites and more traps, the curves diverged. The number of species with intermediate recording frequencies did not change substantially but the number of species with small recording frequencies as well as those with large ones rapidly increased. The curves based on the equal capture probabilities of species remained unimodal when increasing the capture probabilities (Fig. 5). In contrast, the curves based on species records from the field became more and more bimodal when increasing the effort of recording and, therefore, the recording probabilities of the species (Fig. 8).

In the example of Figure 8a, ten species could be found in each spatial sample of a study that was performed with four traps per site. Consequently, in this study these species had a recording probability of $p = 1$. This means that at least one individual of the species was recorded in one of the traps. When using only one of the traps per site, two of the species were nevertheless recorded in each sample (Fig. 8b). This results from the fact that one specimen in the trap is one species record as well as 100 specimens. Hence, the recording probability of an abundant or very mobile species stayed close to one for a wide range of effort and capture probabilities of individuals. On the other hand, the species community shown in Figure 8 also included a substantial number of rare and hardly recorded species, which appeared more and more in the samples with increasing effort. It can be concluded that this is a very basic fact, because it is impossible to record even the rarest species regularly.

The data on epigeal spiders and carabid beetles can be used spatially as well as temporally (see Chapter 3.2.3). In an example from epigeal spiders the data were used with sites as samples (Fig. 9). The values of the recording frequencies tended to be stable at both ends of the curve but differed in

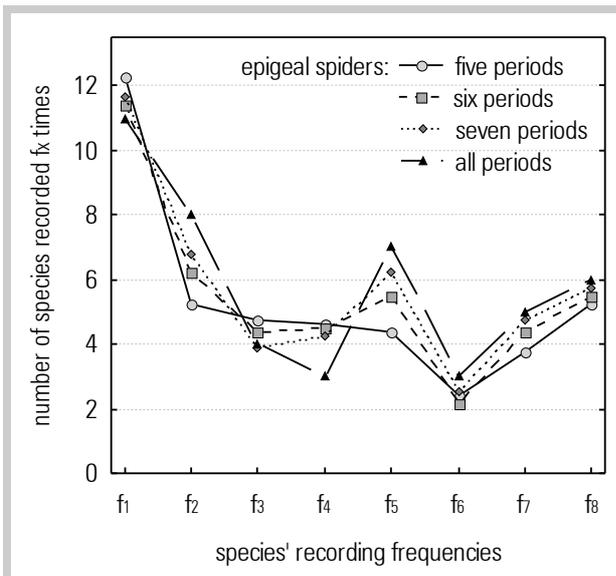


Fig. 9 Distributions of species' recording frequency due to an increasing number of heterogeneous periods.

the central part (Fig. 9) when changing the effort by increasing the number of periods used. The number of abundant species increased slowly with effort. However, the main change occurred in the number of species recorded five times. A possible explanation for this difference from the normal development of the curve with increasing effort is that some of the species appeared on only five of the sampling sites. Thus, the recording probabilities of the sites were seemingly unequal. Different kinds of heterogeneity are addressed in Chapter 3.3.4.

The four sampling periods of two years are used to illustrate the effect of sampling effort

on the distribution of recording frequencies in molluscs. The data originated from 11 moist sites which were used as spatial samples. The mollusc community of these study sites had a small number of species. Nevertheless, with their distribution of recording frequencies the species showed a wide range of recording probabilities (Fig. 10). One species was found in each sample even when using only one field period. As the recording frequencies in the central part of the curve only fluctuated for about two species, this variability was possibly just a random effect. With increasing recording effort, the maximum number of species moved from f_1 towards f_2 (Fig. 10). This could be observed in the molluscs because their species number is small and the communities are closed over longer periods which made it possible to pool samples over years. Such a thing occurs, if the effort becomes high enough to record even species with a very small capture probability more regularly.

The example of the plants showed that an increased effort in recording species does not necessarily lead to a bimodal distribution of recording frequencies (Fig. 11). The number of species with only one record increased drasti-

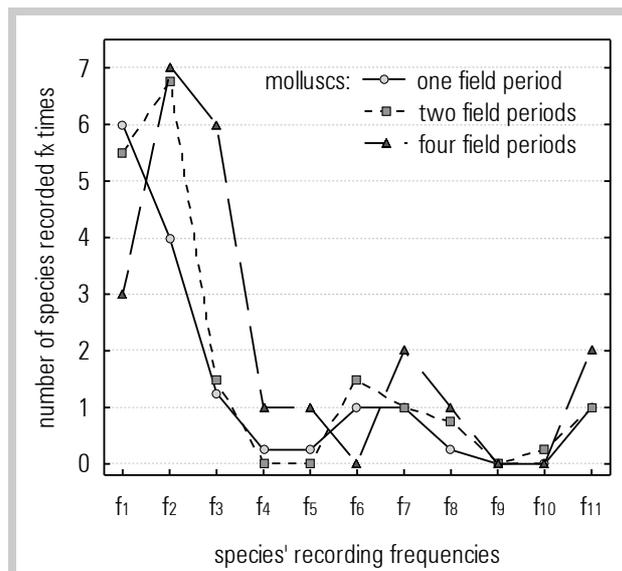


Fig. 10 Distributions of species' recording frequency due to an increasing number of heterogeneous periods.

cally when using a larger plot size, whereas the number of regularly recorded species remained about the same. Thus, the number of recorded species increased, however, the curve shape of the distribution of species' recording frequencies hardly changed. Unfortunately, it cannot be gathered from the field data whether the effort was not high enough to get a bimodal distribution of species' recording frequencies or whether other factors hindered this.

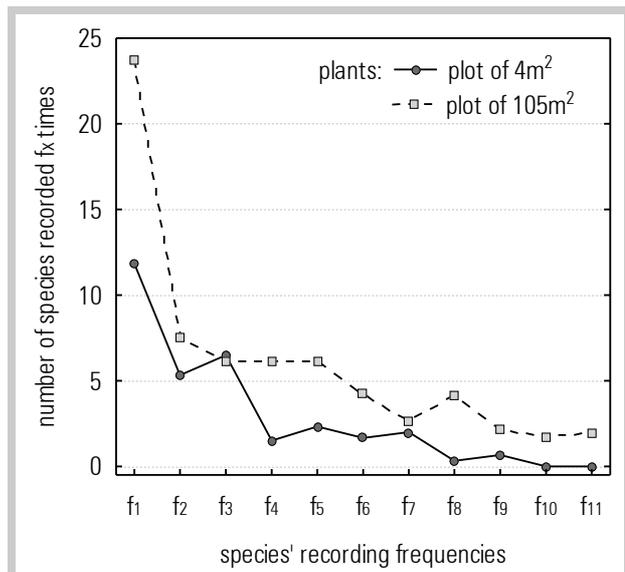


Fig. 11 Distributions of species' recording frequency due to an increasing plot size of the sampling plots.

3.3.3 Species group and habitat

Another group of factors which may affect the distribution of the recording frequencies and, hence, its curve shapes, are characteristics of the species groups. In order to evaluate this influence, samples of species records with a high recording effort were taken from all species groups. The species records originate from the same six study sites and the same study periods. Whereas the curve shapes of the distributions of the three invertebrate groups were more or less clearly bimodal, that of the plants was

unimodal (Fig. 12). This shows that under similar recording conditions the relations of the numbers of rarely and regularly recorded species differed between the studied communities of species groups. As the methods to record these species groups were different, it can not be differentiated with the field data whether the differences were mainly an effect of the characteristics from the species group or of the methods used to record them.

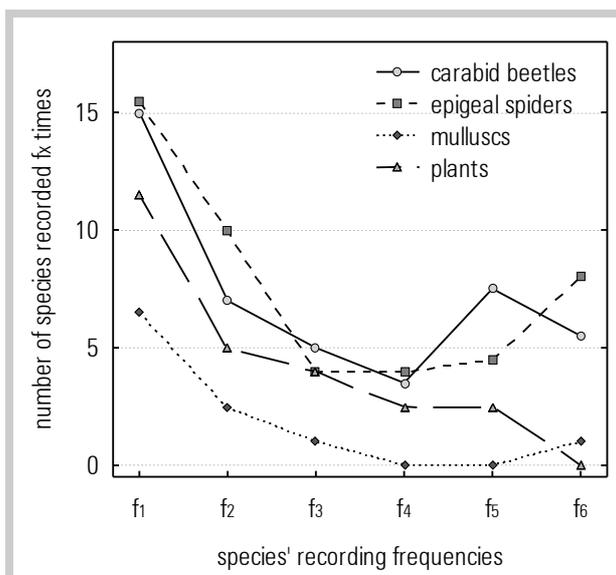


Fig. 12 Distributions of recording frequencies of four species groups recorded with similar effort and on the same sites and periods.

If the number of species from a sampled community affects the curve shape of the distribution of species' recording frequencies, a comparison of species groups with clearly different numbers of recorded species should re-

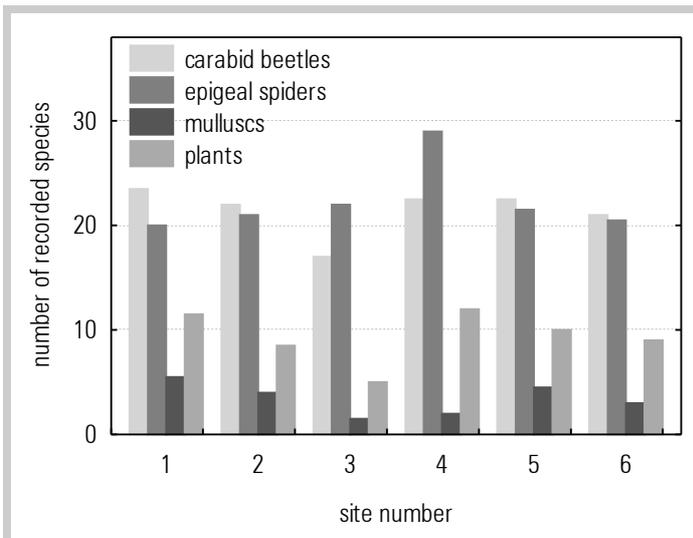


Fig. 13 Numbers of recorded species from six very similar sites.

veal this. The number of species recorded at six similar study sites showed such differences (Fig. 13). The molluscs with the least number of species had a bimodal curve shape for the distribution of species' recording frequencies just like the epigeal spiders and the carabid beetles with much higher species numbers (Fig. 12). In contrast, the species group with an intermediate number of species records i.e. the plants (Fig. 13) had an unimodal curve (Fig. 12). Thus, the number of recorded species did not

seem to affect the curve shape of the distribution of the recording frequencies.

Comparing the frequencies of species records for the same species group, the curve shapes and the species numbers in the samples may be different depending on the habitat type they originate from. On the wet sites, the number of recorded species was usually higher, whereas on the dry sites a few species appeared more regularly (Fig. 14). Thus, the curve shape of the distribution of the species' recording frequencies was unimodal for the species community on wet sites, whereas it was only slightly bimodal for the dry sites. A characteristic of a species group can be for example to be preferably distributed in wet habitats. It can be concluded that this is one possible underlying reason for the differences in the distributions of species' recording frequencies, which are related to habitat factors.

The examples highlighted differences between species groups, especially the complex effects of species characteristics and habitat factors. However, the field data provided a variety of different combinations of species groups and

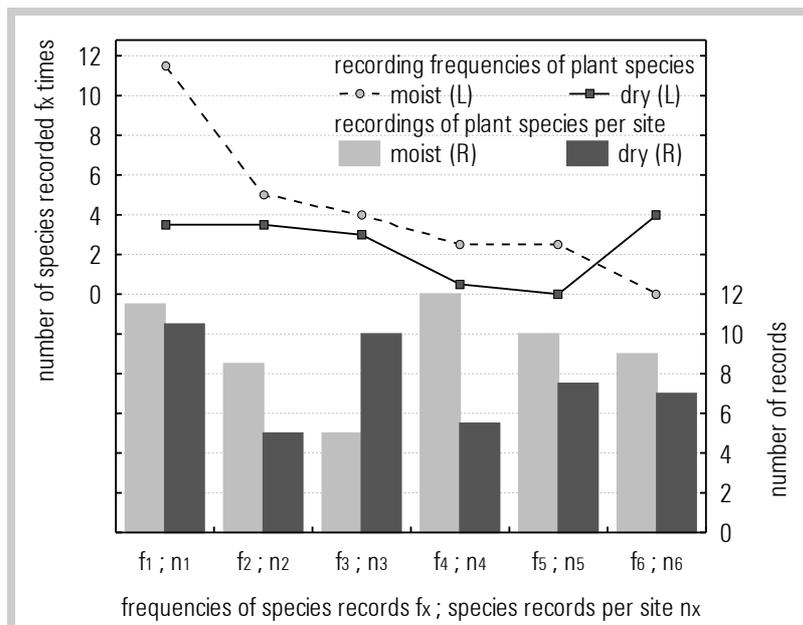


Fig. 14 Recording frequencies and numbers of records of plant species for two groups of sites with different habitat types in terms of moisture.

habitat with similar distributions of species' recording frequencies.

3.3.4 Heterogeneity of sites and periods

The short-term sampling in carabid beetles provided species records from five groups of sampling periods and six groups of sampling sites, which were pooled to provide 30 spatial and 30 temporal mark-recapture-like data sets. These allowed for looking for spatial or temporal heterogeneity among samples. Without heterogeneity caused by differences between sites or periods, in spatial or temporal samples, the number of recorded species per sample ($n_1...n_x$) can be expected to be equal. Therefore, the Chi^2 test could be used to test for deviations from equal recordability caused by spatial and temporal heterogeneity.

Nearly one third of these data sets showed a significant difference ($p < 0.05$) to equal numbers of species records in the samples. Seven of them were spatial samples and twelve of them were temporal. Moreover, the Chi^2 test is probably not very powerful in this case because the number of sites or periods was only six or eight. Usually the coefficient of variation of the species records of the samples was higher when using the data temporally. This means that the differences between the sites of the 60 examples from carabid beetles were mostly smaller than that of the periods. Spatial or temporal heterogeneity was obviously common in samples of species records.

A comparison of two different site groups for the same sampling period showed (Tab. 1) that either spatial or temporal heterogeneity can be stronger and, hence, statistically significant. Accordingly, the coefficients of variation of species records were

Tab. 1 Records of carabid beetles from the same study period, and different site groups.

		number of recorded species	number of species' records	coefficient of variation	significance of the Chi^2 test
site group 2	spatial	31	76	0.47	0.02
	temporal	31	115	0.30	0.23
site group 3	spatial	30	96	0.25	0.62
	temporal	30	109	0.43	0.02

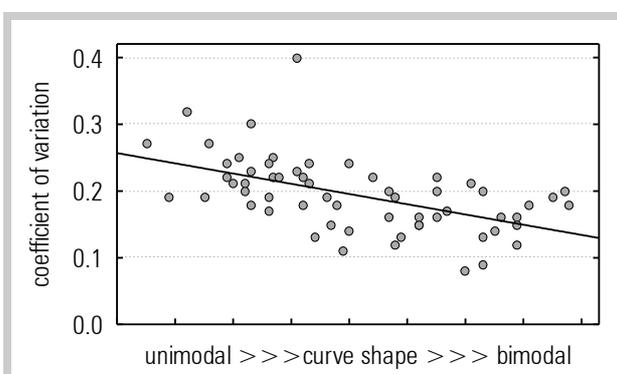


Fig. 15 Correlation of the coefficient of variation and the curve shape of the distribution of species' recording frequencies in epigeal spiders.

higher in the two cases with significant heterogeneity compared to those in the non-significant cases.

The effect of this spatial or temporal heterogeneity on the distribution of species' recording frequencies was analyzed by correlating the coefficient of variation of the species records to an index which expresses the ratio of the numbers of rarely recorded species to frequently recorded species and, consequently, the curve shape of the distribution of

species' recording frequencies. A Spearman's rank correlation test was based on the 60 data sets of carabid beetles from above and on additional 60 sets of epigeal spiders, used for groups of similar sites or periods. The higher the heterogeneity expressed as coefficient of variation was, the more unimodal the distribution of the recording frequencies with an increasing majority of the species on the side with the low frequencies (Fig. 15). The correlation between the coefficient of variation of the species' records of the samples and the curve shape of the distribution of the species' recording frequencies was always significant ($p < 0.05$) even though it was higher for the epigeal spiders (Fig. 15) than for the carabid beetles.

Tab. 2 Correlation (Spearman rank correlation) of number of species records and two weather factors based on data from all study sites on which short term sampling was performed. Grey: significant correlation.

	sampling period	N	maximum air temperature		minimum relative air humidity	
			R	p	R	p
carabid beetles	2	8	0.786	0.021	-0.833	0.010
	3	7	0.500	0.253	-0.250	0.589
	5	8	0.759	0.029	-0.819	0.013
epigeal spiders	2	8	0.634	0.091	-0.878	0.004
	3	7	0.857	0.014	-0.821	0.023
	5	8	0.313	0.450	-0.361	0.379

Temporal heterogeneity, which usually turned out to be higher for the short-term periods, can be caused by differences in weather factors like air temperature and relative air humidity. These factors were measured close to the study sites and, hence, could be correlated

with the number of recorded species for the single two-day periods. In spite of the low number of samples, the maximum air temperature and the minimum relative air humidity correlated with the number of species, which were recorded on the 20 sites over the single short-term periods (Tab. 2). On physical grounds, the higher the maximum air temperature was, the lower the minimum relative air humidity. Thus, the positive values of R for the maximum air temperature (Tab. 2) and the negative values of R for the minimum relative air humidity (Tab. 2) mean the same. In conclusion, weather conditions affected the number of species records and caused heterogeneity in the recording probability of species among sampling periods.

The basic samples of the distributions and later on for the species richness estimation are the species records of sites and periods respectively. Thus, pooling different species groups both spatially and

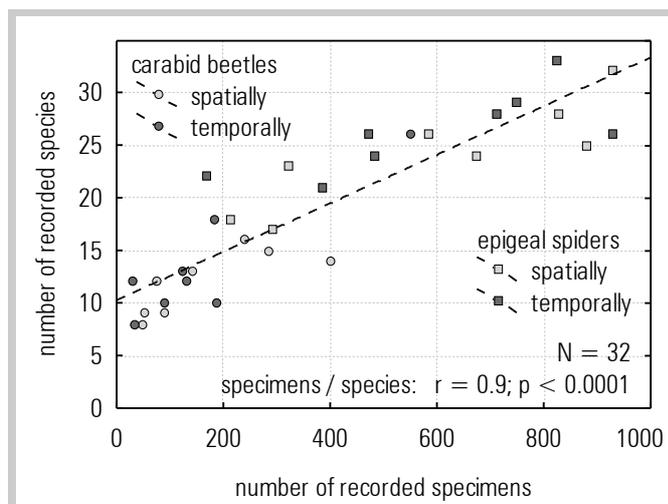


Fig. 16 Correlation of numbers of captured specimens and recorded species.

temporally, the numbers of recorded specimens was significantly correlated with the number of recorded species (Fig. 16).

Although the numbers of specimens caught and the numbers of species recorded were correlated both in spatially and in temporally pooled samples, these correlations were not related to one another. This is illustrated by an example of epigeal spiders with eight short-term samples from one period from a group of eight similar sites. In this case the numbers of trapped specimens and the

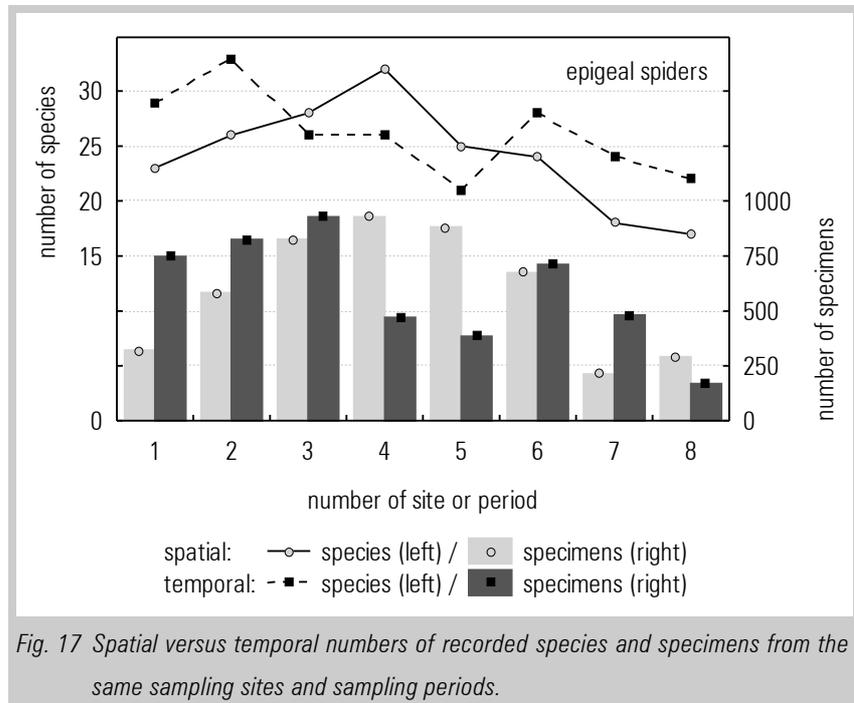


Fig. 17 Spatial versus temporal numbers of recorded species and specimens from the same sampling sites and sampling periods.

numbers of recorded species of the eight samples were significantly correlated (spatially: $p = 0.007$, temporally $p = 0.031$; Spearman rank correlation). These correlations were caused by linked variations of recording probability (Fig. 17). However, spatial and temporal numbers of recorded species as well as numbers of trapped specimens (Fig. 17) were not significantly correlated (species: $p = 0.51$, specimens: $p = 0.96$; Spearman rank correlation). Thus, the differences in the general recording probabilities of spatial and temporal samples were unrelated.

3.4 Discussion

There is a number of examples of inventories with quantitative sampling in several species groups, such as ants (LONGINO ET AL. 2002), spiders (CODDINGTON ET AL. 1996), plants (SKOV & LAWESSON 2000), parasites (WALTHER & MORAND 1998), and, particularly, birds (SOBERÓN & LLORENTE 1993, DAWSON ET AL. 1995, NICHOLS ET AL. 1998A, CAM ET AL. 2000). Many of them cover large areas and hence several habitats, which means that the recording probability of the species varies widely from sample to sample. In most of these studies species richness estimators are used, which are based on recording frequencies, (BURNHAM & OVERTON 1978, BURNHAM & OVERTON 1979, CHAO 1984, CHAO ET AL. 1992). Consequently, the distribution of the species' recording frequencies affects the accuracy and reliability of these estimators. Nevertheless, the distribution of the species' recording frequencies is not shown except in CODDINGTON ET AL. (1996), who reported from their inventory on spiders that the distributions of species' recording fre-

quencies are slightly bimodal. Thus, the factors affecting this distribution need to be discussed.

3.4.1 *Methods of sampling species*

Most of the estimators of species richness were originally developed for estimating population size. Data collected for this task are mainly temporal and are sampled during consecutive periods with the mark-recapture design. All the inventories cited above were conducted spatially on numerous more or less unequal sites. However, the differences between spatial and temporal sampling are not discussed. In this study, it was the first time a design had been chosen (see Chapter 3.2.3), which enabled a comparison between spatial and temporal sampling in terms of the shape of the distribution of the species' recording frequencies and, hence, the accuracy and reliability of species richness estimates.

The advantage of the sampling design of this study was the possibility to use the same trapping results as spatial and temporal samples. These comparisons showed that the curve shapes of the distributions of recording frequencies from the same trapping data can clearly vary between spatial and temporal use. However, no consistent difference between the curve shapes of spatial versus temporal sampling could be detected. The type of curve shapes from the distributions was basically the same. Moreover, spatial and temporal heterogeneity in the samples were unrelated. BURNHAM & OVERTON (1979) stated that each sampling design with a defined number of identified units of equal effort is suitable for their nonparametric species richness estimators. This is confirmed in that no fundamental difference between the curve shapes of distributions of species' recording frequencies from spatial versus temporal sampling could be found.

In contrast to a spatial design, a frequent emptying of traps is necessary, when using a temporal sampling design for trapping animals. It could be assumed that this frequent emptying affects the trapping results. However, in this study no such effect could be found. Thus, there is no need to avoid the temporal sampling design because of the effect from frequent trapping.

3.4.2 *Influences on recording frequency distributions*

The basic data set for mark-recapture methods, when using them to estimate species richness, is a condensed history of species records, the distribution of the species' recording frequencies (OTIS ET AL. 1978). The underlying distribution is that of the species' recording probabilities. The recording probability of a species is defined as the probability of a species being found with at least one individual in a sample taken from any kind of field work (BURNHAM & OVERTON 1979). These recording probabilities of the species of a community are usually unknown and depend on the recordability and the abundance of the species, as well as on sampling effort in the field.

Many of the distributions of species' recording probabilities of this study were bimodal. As

CODDINGTON ET AL. (1996) reported the same for spiders, the shape of the frequency distribution curve does not appear to be unusual in data sampled for species richness estimation. From this study it can be concluded that the distributions of species' recording frequencies is usually bimodal if the recording effort is adequate, because in order to get species with small recording probabilities, the recording effort must always be high enough so that the abundant species are regularly found in the samples. Hence, it is impossible to get an even roughly equal recording probability by increasing the recording effort in the field. Consequently, the additional species occurring with higher effort have always belonged to the community and the increase of the recorded species number is no evidence that the species community is not closed.

On the one hand species have different recording probabilities (COLWELL & CODDINGTON 1994, BOULINIER ET AL. 1998). On the other hand, the effort, which is invested in recording the species in the field mainly affects the probability of each species of a community to being trapped and, hence, becoming a member of a sample. If a species community consisted of species all having the same capture probability, the distributions of recording frequencies would change with increasing effort as shown in Figure 5. As expected, the distributions of species' recording frequencies in this study differed from this pattern. Thus, they confirmed that the species of a community have a wide range of capture probabilities.

In this study, the distributions of recording frequencies from the same sampling survey partly showed differences between species groups. In ecology, terms like dominance and evenness are used to characterize the ratio of specimens that belong to each of the species of a community (BEGON ET AL. 1990). In this respect, species groups can be different and one species group can vary in different habitats. Thus, it can be concluded that dominance and habitat use, which are components of the characteristics of species groups, affect the distributions of recording frequencies.

If the samples originate from a spatially and temporally homogeneous species community an increased effort made the curve shape more bimodal and the number of rare species as well as the number of abundant species increased. However, if an increasing number of samples resulted in an increasing number of sampled habitats and, hence, in increasing spatial heterogeneity, the number of abundant species stayed constant, whereas the number of rare species continued to rise. The example with the plants demonstrated this (see Chapter 3.3.2). On the one hand, a vegetation plot of 4 m² is usually too small to include all species of a plant community. On the other hand, a really homogeneous site in the field is a very rare thing, hence, a vegetation plot of 105 m² usually covers larger parts of a habitat gradient occurring on the study site. Thus, spatial heterogeneity provides an obvious explanation for little change in the curve shape of the distribution of species' recording frequencies in spite of clearly increasing effort.

Air temperature and relative air humidity affected the recording probability of carabid beetles and epigeal spiders in this study and, hence, caused temporal heterogeneity. This is understandable, be-

cause these weather parameters are important factors for the activity of invertebrates (HONEK 1997). Therefore, the global recording probability of trapping periods was relatively high in warm sampling periods and lower in cooler ones. The coefficients of variation of the number of recorded species from seemingly homogeneous sites and periods showed similar values. This means that the general recording probability of sites and periods was similarly variable. Thus, the curve shapes of the recording frequency distributions can be affected by both of the sources of heterogeneity to a similar degree.

In order to be able to interpret the distributions of the species' recording frequencies, additional factors must be considered. In case of traps, catchability is a mixture of behavioral factors according to habitat structure and weather, the activity and mobility of the species, and the trapping method. For example, small species are more in danger of drying out than large ones. Hence, at high temperatures, small species in particular tend to avoid traps which are not covered by vegetation (HONEK 1997). Adversely, some preservatives, formalin or ethylene glycol for example, attract some species (HOLOPAINEN 1992, TEICHMANN 1994) and thus affect the recording probabilities.

In summary, sampling effort, characteristics of the species groups, and spatial as well as temporal heterogeneity caused by differences in the study sites and periods affected the distribution of species' recording frequencies in a complex way. However, the effects of the single factors and their significance in different situations could not be singled out and determined from the field data. Thus, only a simulation, albeit based on these results, can sufficiently clarify the role of these single factors.

3.4.3 Abundance distribution and recording probability of specimens

The factors discussed above clearly affect the curve shape of the distributions of species' recording frequencies. Nevertheless, the shape of this curve is basically ruled by the distribution of species' recording probabilities. The abundance distribution of the species of a community reflects their relative recording probabilities. In this study the most frequently recorded species were represented by some hundred times more specimens than the rarest. In agreement with this, CODDINGTON ET AL. (1996) reported that abundances of species covered about eight octaves. This also means that the most abundant species are recorded 250 to 500 times more frequently than the rarest. Thus, it is useful to discuss distributions of species abundances in the light of their effect on the distributions of species' recording frequencies.

In community ecology, species abundance distributions have been a topic of interest for a long time (ENGEN 1978, TOKESHI 1993). In order to be able to use this basic knowledge about species communities in models, ecologists as well as statisticians have tried to fit them to a number of distributions (MAY 1980, TOKESHI 1993, ENGEN & LANDE 1996). As the population size of all these species is not known, an absolute capture probability cannot be derived. Additionally, the exact shape of the distribution depends on characteristics of the species group, the unknown abundances of each of the species, the trapping

method and the trapping effort. These various factors have prevented establishing a reliable approach to select one of the proposed distributions (MAY 1980, TOKESHI 1993, ENGEN & LANDE 1996) of abundance distributions for modeling.

It can be expected that lognormal distributions should fit the species abundance distribution, if sampling is performed in really homogeneous space and time and without succession like in a single sample of diatoms (MAY 1980). Several gamma distributions fit the spatial or temporal distribution of the species abundance, if the sampling area or sampling period contains more or less heterogeneity. For example bird communities of whole islands (MAC ARTHUR & WILSON 1967) are always drawn from spatially heterogeneous areas, which means that not all species have the same probability of being recorded at each point on the island. ENGEN & LANDE (1996) derived from a special gamma model that the underlying distribution of recording probabilities must be an exponential distribution, which also underlies the broken stick model.

The selected examples as well as the whole species recording data of this study confirmed previous observations (BURNHAM & OVERTON 1979, COLWELL & CODDINGTON 1994, BOULINIER ET AL. 1998) that the majority of species are more or less rarely recorded and only a few are recorded regularly. This species abundance distribution reflects the distribution of species' recording probabilities. Hence, a function modeling this distribution must have its maximum on the left side, where all the rarely recorded species can be found. The density function of the exponential distribution ($f(x) = e^{-x}$) meets this condition.

As recording probabilities are significantly affected by the species' abundances, and the abundances are found to be exponentially distributed in species communities (ENGEN & LANDE 1996), the density function of the exponential distribution can serve as the underlying distribution of the species' recording probabilities in simulations used to test species richness estimators.

4 Factors affecting species' recording frequencies in simulation

4.1 Introduction

Distributions of species' recording frequencies are the result of species characteristics like abundance as well as mobility and factors like sampling effort or heterogeneity of study sites and periods (see Chapter 3.3). In field data, these factors cannot usually be recorded separately. Thus, a simulation is needed to separately study their effects on the distribution of species' recording frequencies. Nevertheless, this requires field data to get realistic and reliable assumptions about the values and effects of these factors on the distributions of species' recording frequencies.

The basic concept of this study is to compare the accuracy and reliability of species richness estimators. Species richness estimators are based on species' recording frequencies, at least f_1 (BURNHAM & OVERTON 1978), f_1 and f_2 (BURNHAM & OVERTON 1978, CHAO 1984), or more of the recording frequencies (CHAO ET AL. 1992) and the number of species records (OTIS ET AL. 1978, CHAO ET AL. 1992). Thus, the curve shape of the distribution of species' recording frequencies can be used to evaluate whether the assumptions and, hence, the parameter settings of the simulations are realistic. This evaluation is crucial to get a useful analysis of the accuracy and reliability of the species richness estimators. Thus, knowing how factors like sampling effort, characteristics of the species group or heterogeneity of study sites and periods affect the distributions of species' recording frequencies and the number (of incidences) of species records is the link to understand how these factors affect the accuracy and reliability of the species richness estimators.

Some theoretical distributions were applied to model distributions of recording frequencies (BURNHAM & OVERTON 1979, CHAO 1987, CHAO ET AL. 2001). However, these reflect the result of complex interactions of factors like sampling effort, characteristics of species groups or heterogeneity of study sites and periods but their effects cannot be differentiated. In order to separately study the effects of these factors on the distribution of species' recording frequencies, they have to be under control. Moreover, a basic distribution of the probabilities of a specimen being recorded at one site and over one period is needed for each of the species. This distribution has to provide a rough range of the differences of species' recordabilities caused by their differences in abundance and mobility (see Chapter 3.4.3). Then, based on such a fixed distribution, the influence of the factors mentioned above on the curve shape of the distribution of species' recording frequencies can be separately studied. Thus, a simple model is used to provide basic species' recording probabilities.

The examples from the field data (see Chapter 3.3) showed some factors to affect the curve shape of the distribution of species' recording frequencies. Thus, the aim of this chapter is to show by simulations, how separate factors like sampling effort, characteristics of the species group or heterogeneity of study sites and periods affect the distribution of species' recording frequencies.

4.2 Methods

4.2.1 Simulation

The basic data of species richness estimation are species lists of sampling sites and sampling periods. These species lists are summed up from single events of animals being trapped or plants being found. In the simulation a virtual species in a virtual trap is recorded, if a random number between zero and one is equal to or smaller than the species' probability of being recorded. This is the basic incident on which every virtual history of species records was constructed. The basic settings of the simulations were the number of species, the number of periods of trapping, and the number of sites, each with a number of traps. All these factors are variable and had to be set to useful and plausible scenarios. Although the simulation program allows for an adjustment of the number of repeats for each simulation run, in the study 1000 repeats were always used.

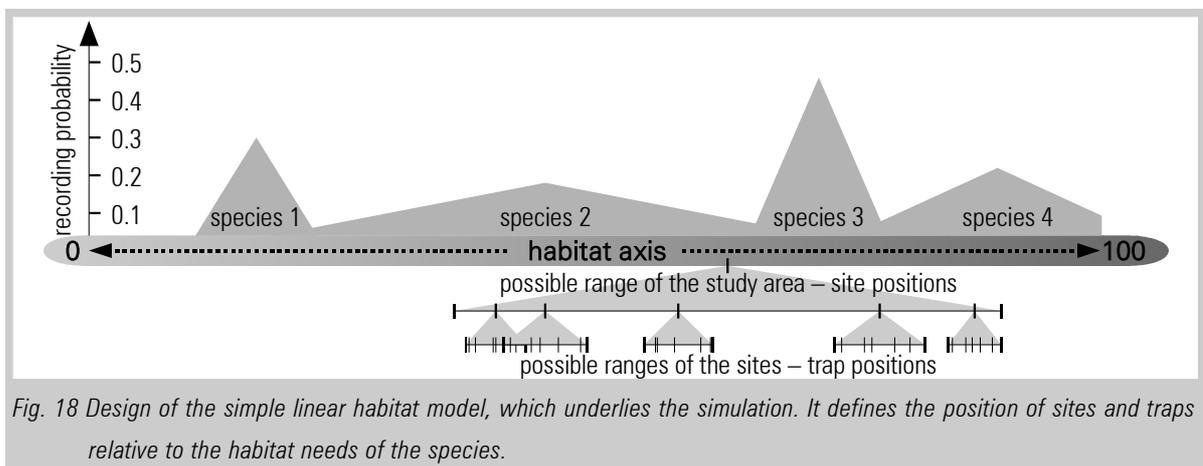


Fig. 18 Design of the simple linear habitat model, which underlies the simulation. It defines the position of sites and traps relative to the habitat needs of the species.

In order to model differences in habitat preferences of species and differences in traps and sites, a habitat axis was developed. This is a one-dimensional habitat gradient, on which each of the species has its ecological range and on which every trap is placed (Fig. 18). It has a scale from 1 to 100 without any ecological meaning. However, this scale indicates that the environment in which the species can be recorded with traps is not homogeneous.

Each of the species was defined by a maximum recording probability, a position of this maximum on the habitat axis, and a breadth of its niche. This niche breadth was defined by the points on the habitat axis, where the linear decreasing recording probability, which started at the point of its maximum, reached zero (Fig. 18). All values were set at random within ranges which were separately defined for each group of simulation runs. The study area of every simulation run covered only a fraction of the habitat axis. Within this study area the sites, and within the sites the traps, were placed randomly. This way, every trap obtained a definite position on the habitat axis (Fig. 18). Therefore, all species had a definite probability of being recorded at the definite positions of each of the traps.

Usually, species lists of community studies consist of the records of one site, not of one trap. Therefore, in the simulation one record in one trap created one record at the site as did five records in five traps. In this way, different efforts per site from one to many traps could be simulated. The effort in terms of duration of the study periods was always realized by changing the number of periods but never by changing the duration of the single periods. As the basic recording probability is related to one trap and one period, changing the duration of the single periods would have corresponded to changing the basic recording probability of the species.

Each result from trapping during a simulation consisted of a number of species lists, which could be pooled either spatially or temporally. Spatially implies that the species lists of the periods were pooled for each site, whereas temporally implies that the species lists of the sites were pooled for each period. Both kinds of pooling were applied in every simulation run.

4.2.2 Heterogeneity in the simulation

Heterogeneity of species' capture probabilities has three different sources. Species are different in population size, in activity and in the use of habitats, periods are different for example in weather conditions, and sites and traps respectively are different in their position on the habitat gradient and with factors like vegetation influencing their efficiency. Table 3 provides an overview of the parameters used and their default values in the simulation.

The field data made it obvious (see Chapter 3.3) that the majority of species are more or less rarely recorded and only a few are recorded regularly. Hence, a function modeling the basic distribution of the recording probabilities must have its maximum on the left, where all the rarely recorded species

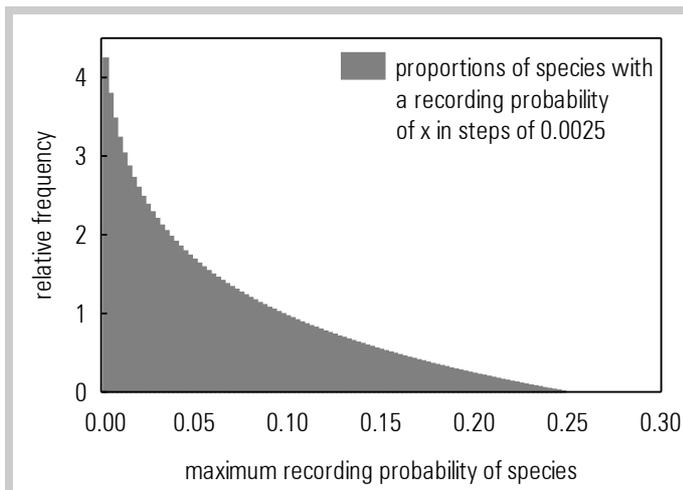


Fig. 19 Distribution of the relative frequencies of species' recording probabilities used in the simulation while dividing the range of the recording probabilities in 100 equal fractions.

can be found. Hence, the density function of the exponential distribution ($f(x) = e^{-x}$) can serve as the basis of a simulation to investigate the effects of species group, trapping method, and trapping effort (see Chapter 3.4.3). The curve started with a fraction of p_{max} defined by $e^{-x} * p_{max}$ with the exponent x (in this study: $x = 4.7$) and ends with $e^0 * p_{max}$ and a predefined general maximum recording probability (in this study: $p_{max} = 0.25$). The distribution of the proportions of species with definite

maximum recording probabilities in Figure 19 reflects the probabilities of species in the simulation to be randomly assigned to a recording probability. In this way, each of the species was defined by a maximum probability of being recorded and by a position and a range on the habitat axis (Fig. 18).

In biological terms, the exponent (x) is a measure of how many times smaller the recording probability of the rarest species is than that of the most abundant. In biological terms, the maximum recording probability (P_{max}) is a characteristic of the species group and the method of recording the species. Default values for these two parameters were found by a preliminary simulation with 60 species, eight periods, and constant effort (Fig. 20). In this case constant effort meant that the mean recording probability of the simulated species community was equal in all simulation runs. Thus, the number of species having low and high recording probabilities respectively was

only ruled by $f(x)=e^{-x}$. The distributions of the species' recording frequencies became more bimodal when increasing the range of the species recording probabilities (Fig. 20). Hence, the density function of an exponential distribution provides a good approximation of the distribution of species' recording probabilities, if appropriate values for the exponent are used. The values used were selected by their ability to deliver simulated species' recording frequencies (Fig. 20), which are similar to those found in the field (see Chapter 3.3).

Changes in weather are the most important source of heterogeneity in temporal samples (see Chapter 3.3.4). The recording probabilities of species in a specific trap are affected in two ways: the basic recording probabilities during the periods are different and the density of activity of the species along the habitat axis changes. The first was included in the simulation as a deviation in percentage of the basic recording probability of all species. The second was realized by shifting the single species for a definite percentage along the habitat axis. What happens to a definite species during the periods of a simulation was limited by the settings of scenarios and was chosen at random.

The sites and traps respectively varied in having different positions on the habitat axis and covering different fractions of it (Fig. 18). The scenarios were defined in this case by setting a maximum width as a percentage of the length of the habitat axis. However, one must acknowledge that sites and traps

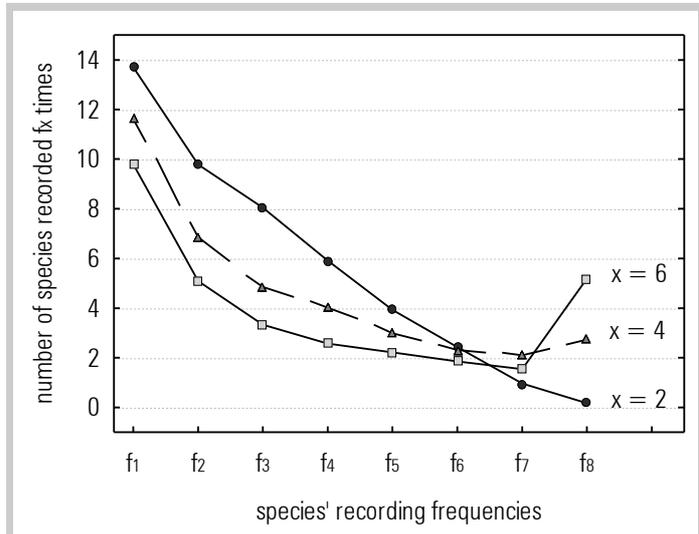


Fig. 20 Dependency of the curve shape of the distribution of species' recording frequencies on powers of e used for modeling the basic distribution of species' recording probabilities.

in the field differ in their effectiveness for reasons that can not be represented on a habitat axis. This heterogeneity was expressed in the simulation as random increases or decreases in the basic recording probability of the traps or sites.

Tab. 3 Values of the basic parameters in the simulation.

number of simulated species	60
number of sessions	8
number of sites	8
number of traps	5
Basic maximum recording probability per trap and session	0.25
exponent (x) expressing the range of the recording probabilities	4.7
maximum deviation of the recording probability (all species)	50 [%]
maximum specific shift on the habitat axis	50 [%]
minimum width of the species range on the habitat axis	5 [%]
maximum width of the species range on the habitat axis	60 [%]
range of the sites as portion of the habitat axis	50 [%]
range of the traps as portion of the habitat axis	10 [%]
maximum deviation of the sites	100 [%]
maximum deviation of the traps	200 [%]

As the number of variables in the simulation is large, it is impossible to run a simulation for each combination of values for the variables. Starting with a basic scenario (Tab. 3), that reflects a typical situation known from the field, most of the variables were kept constant, whereas one variable or a useful group of them was set to increasingly extreme values. In

this way, the effect of the factors on the distributions of recording frequencies could be observed with a limited number of simulations.

4.2.3 Number of species records and curve shape index

The distribution of the recording frequencies of the species of a community is one of the major factors affecting the accuracy and reliability of the estimators because these are based on species' recording frequencies (BURNHAM & OVERTON 1978, BURNHAM & OVERTON 1978, CHAO 1984, CHAO ET AL. 1992). Thus, the ratio of the number of rare versus frequent species which is represented by the curve shape of the distribution of species' recording frequencies is important for the accuracy and reliability of species richness estimators. In order to handle the curve shape of this distribution easily, it is desirable to find a way to reduce this curve into one continuous parameter. For this purpose a "curve shape index" (CSI) was calculated as follows:

$$CSI = \frac{\sum_{i=t/2+1}^t f_i}{\sum_{i=1}^t f_i} - \frac{\sum_{i=1}^{t/2} f_i}{\sum_{i=1}^t f_i}$$

with f_i being the number of species recorded exactly i times in t samples. The CSI reflects the ratio of the recording frequencies with the first term representing the proportion of species with high recording frequencies and the second term representing the species with low recording frequencies. If the number of samples is even, it can easily be separated into two equal parts. If the number of samples is uneven the median sample is omitted. The CSI provides a negative value, if the left part of the

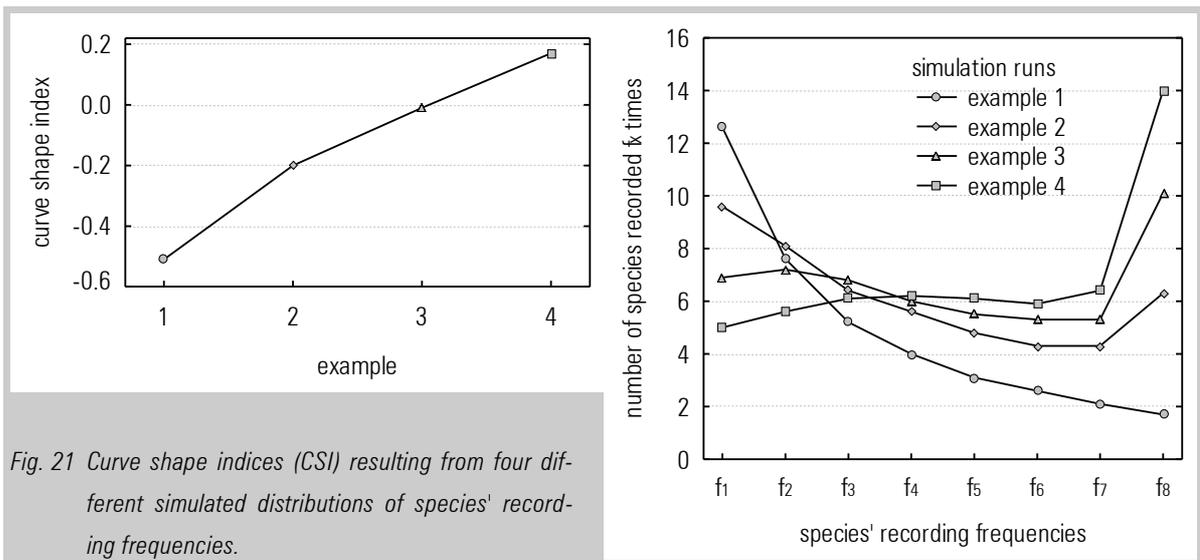


Fig. 21 Curve shape indices (CSI) resulting from four different simulated distributions of species' recording frequencies.

distribution curve of species' recording frequencies is higher than the right, a positive, if it is the other way round, and zero, if both parts are equal. Figure 21 exemplarily shows how the distribution curve of the species' recording frequencies is connected to the curve shape index (CSI).

Another factor, which seems to be important in species richness estimation since it appears in the formulas of some of the estimators (CHAOT ET AL. 1992, OTIS ET AL. 1978), is the number (of incidences) of species records.

$$\sum_{i=1}^t if_i$$

However, this must not to be confused with the number of recorded species.

$$\sum_{i=1}^t f_i$$

4.3 Results

The simulation showed that three main factors affect the shape of the distribution curve of species' recording frequencies: the sampling effort, characteristics of the species groups in their habitats and the extent of variability of the study sites and the study periods respectively. Generally speaking, an increasing effort resulted in an increasing CSI and an increasing number of species records. Heterogeneity in the spatial or temporal samples caused by characteristics of the species groups in their habitats and the variability of sites and periods proved to affect the CSI in a complex way. Generally, the more heterogeneous the samples, the more the CSI decreased and the more the number of species records increased. Combinations of these different sources of heterogeneity of the samples could have an equally strong effect on the CSI and the number of species records like the effort. Species number itself had no effect on the CSI, however, more species resulted in a higher number of species records.

These general results were supported by a number of scenarios of the simulation which were chosen to represent the general results as well as exceptions. First, scenarios with varying effort (4.3.1)

and different sampling designs (4.3.2) are presented. This is followed by various scenarios from individual sources of heterogeneity of species' characteristics in their habitats (4.3.3) and scenarios from spatial and temporal samples (4.3.4). Then the complex effects from various groups of sources of heterogeneity of samples are simultaneously studied (4.3.5). After that, a scenario with different species numbers is presented (4.3.6). Last, the influence of these factors on the number of species records is briefly shown (4.3.7).

4.3.1 Effort

A group of simulation scenarios with increasing numbers (4 to 20) of both sites and periods showed the effect of effort on the distribution of species' recording frequencies. The remaining values took the default values (Tab. 3). The curves of the distributions (Fig. 22a,b) emerged when using the periods as samples. In Figure 22c,d these distributions are represented by one point of the CSI-curve which demonstrates the development of the CSI according to groups of scenarios of increasing effort in terms of an increasing number of both sites and periods.

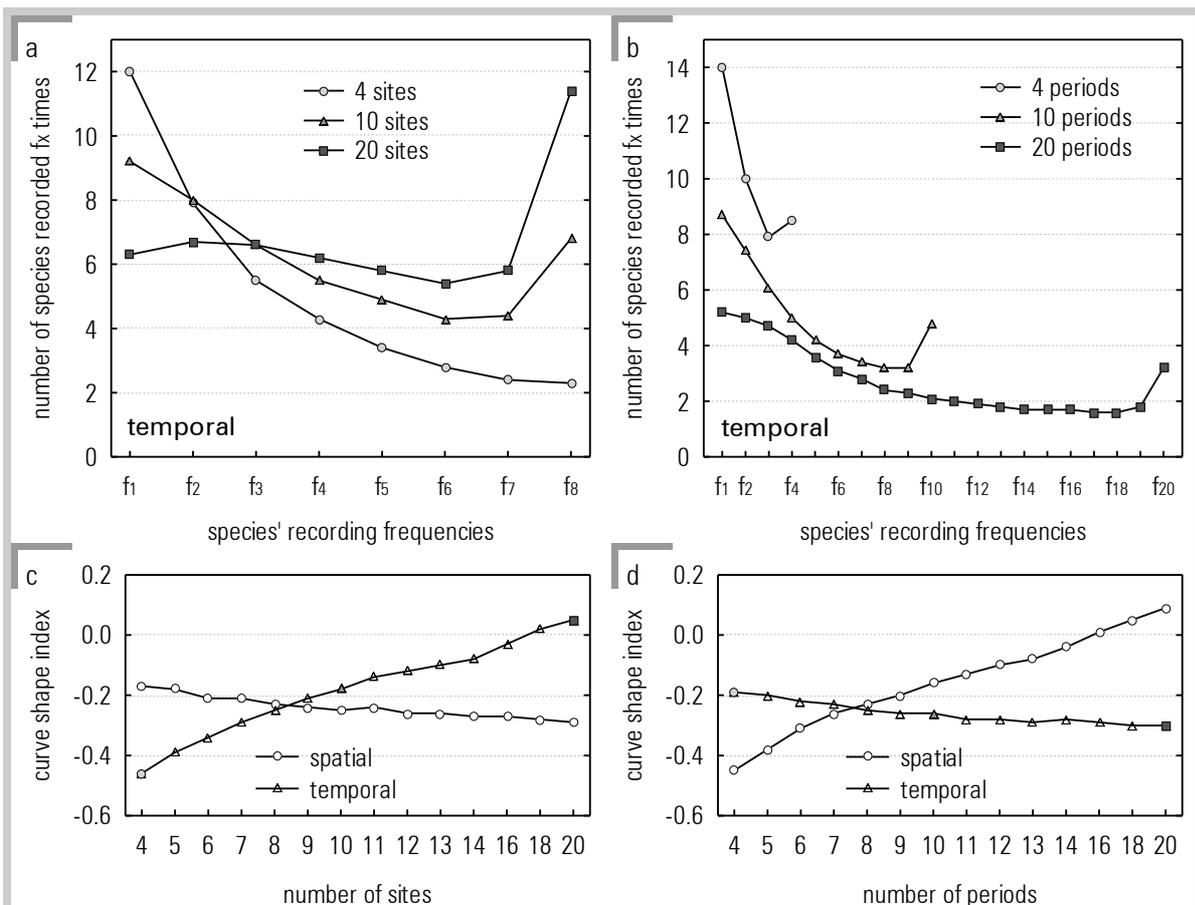


Fig. 22 Changes in the shape of the distribution curve of species' recording frequencies as a consequence of increasing recording effort in terms of increasing numbers of both sites and periods.

In groups of scenarios with an increasing number of sites and periods as samples, the curve shapes of the distributions of species' recording frequencies became more bimodal (Fig. 22a), and the CSI increased (Fig. 22c). However, when increasing the number of periods the curve shapes remained quite similar (Fig. 22b), and the CSI slightly decreased (Fig. 22d). Using periods as samples an increasing number of sites caused an increase in the species' recording probability per period, whereas the recording probability related to one sample remained equal when increasing the number of periods. When using the samples spatially, it was the other way round. Thus, the exact opposite happened to the CSI curves of the scenarios with spatial sampling (Fig. 22c,d). The spatial (Fig. 22c) and the temporal (Fig. 22d) curve of the CSI slightly decreased because the default heterogeneity of the simulation accumulated with the increasing number of sites and periods respectively.

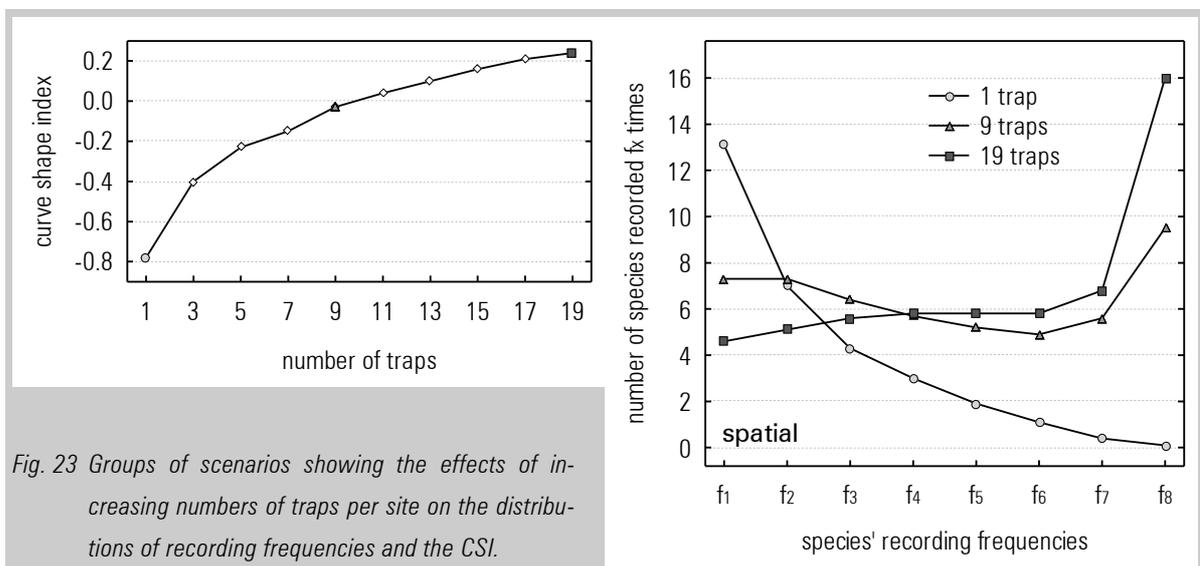


Fig. 23 Groups of scenarios showing the effects of increasing numbers of traps per site on the distributions of recording frequencies and the CSI.

Another group of scenarios represents the effect of increasing effort in terms of an increasing number of traps per site. In this group of scenarios, the increasing effort caused the curve shapes to rapidly become bimodal (Fig. 23). Hence, the CSI rapidly increased with an increasing number of traps per site. In the simulation, sites were selected that were largely homogeneous and, hence, additional traps recorded more of the same species rather than more species.

4.3.2 Sampling design

Two scenarios with increasing numbers of traps differed in terms of the numbers of traps per sampling site, five traps versus one trap per site. The increasing effort caused a parallel increase in the CSI in all groups of scenarios (Fig. 24). Although scenarios with 50 single traps at 50 sites represent the same effort as scenarios with groups of five traps at ten sites, the CSI of the scenarios with the samples of spatially-used single traps was clearly lower than the CSI of the scenarios with five traps grouped per site (Fig. 24). This difference between the two curves of spatial sampling originated from

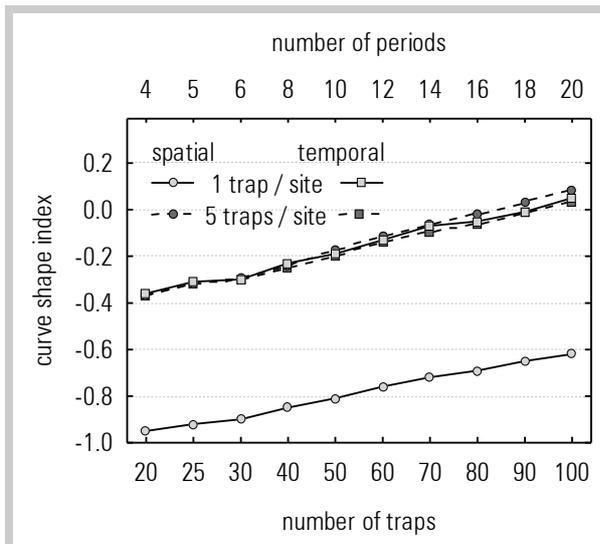


Fig. 24 Groups of scenarios with increasing numbers of traps and periods respectively with traps used singly versus in groups of five traps per site.

the fact that single traps cover more of the variability of a study area than groups of five traps. When using the samples temporally, no difference in the CSI could be observed (Fig. 24), because the differences in the spatial heterogeneity covered do not affect the temporal samples.

Options of sampling design were studied in a group of scenarios with constant effort and similar temporal and spatial heterogeneity. In these scenarios, the numbers of sites and periods were varied from 4 sites with 16 periods to 16 sites with 4 periods (Fig. 25). The distributions of the species' recording frequencies were very similar and the CSI-curves were mirror images

of each other. Using a small number of samples the CSI was low and vice versa. Thus, it can be concluded that under the condition of similar heterogeneity of sites and periods, spatial and temporal designs of sampling are equivalent.

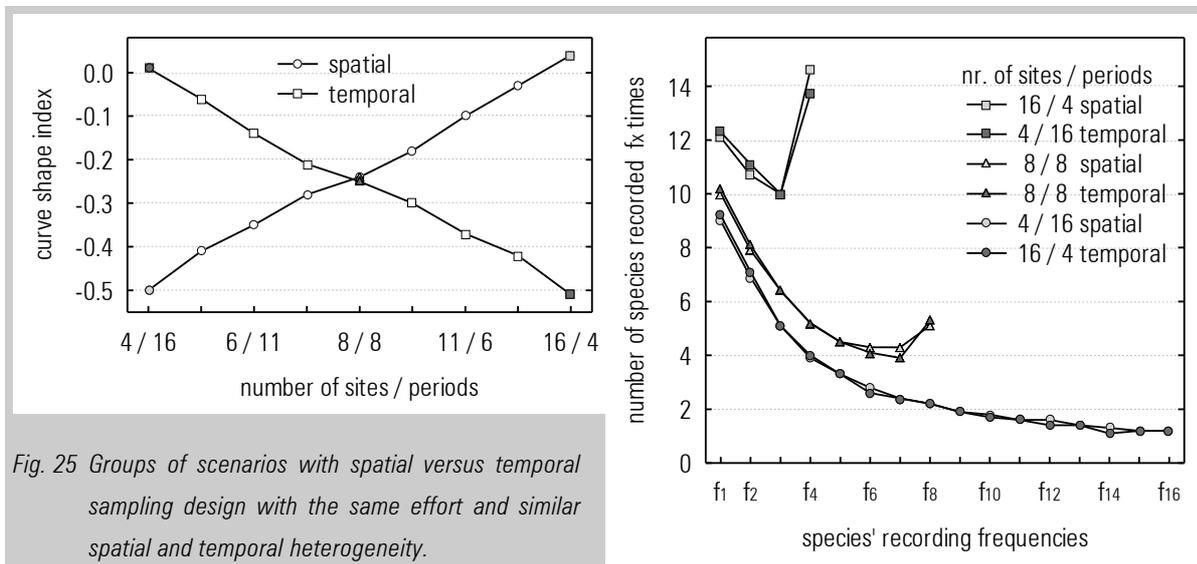


Fig. 25 Groups of scenarios with spatial versus temporal sampling design with the same effort and similar spatial and temporal heterogeneity.

4.3.3 Niche width

Heterogeneity in samples caused by the range of habitat factors in which a species can be recorded is studied by groups of scenarios which operate this to change. Increasing the maximum niche width with constant minimum niche width, the CSI drastically increased (Fig. 26). Increasing the minimum

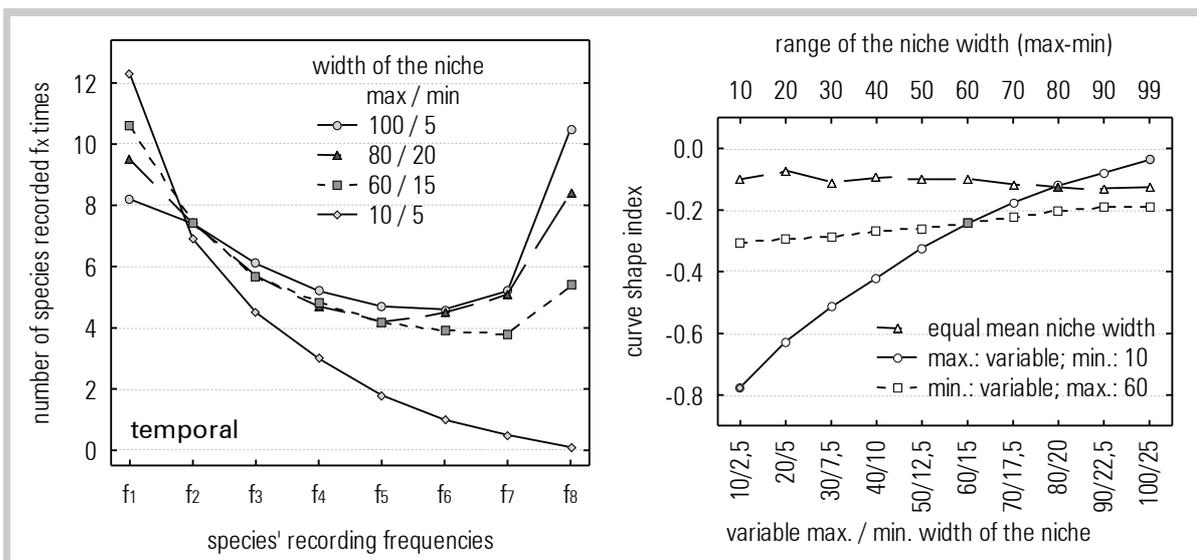


Fig. 26 Groups of scenarios with varying maximum niche width, minimum niche width, and range of the niche width with constant mean niche width. The gray marked points in the CSI curves refer to the distribution curves.

niche width with constant maximum niche width, the CSI also slightly increased. In both groups of scenarios the ratio of generalists (wide niche width) to specialists (small niche width) moved towards the generalists. Thus, increasing the maximum niche width clearly increased the mean recording probability of the species. When increasing the minimum niche width the mean recording probability changed less, partly, because of the smaller steps used in the simulation to increase the minimum niche width. Thus, the CSI values increased because in the mean the species of the simulated communities became more generalist (Fig. 26). This caused increasing mean recording probabilities, and in particular a higher number of regularly recorded species.

In the third group of scenarios the range of niche widths of the species varied, whereas the mean niche widths were kept constant and, hence, the mean recording probabilities of the species. The increasing range between the minimum and the maximum niche width only marginally altered the CSI (Fig. 26). Thus, it can be concluded that the distribution of the recording frequencies is affected by the ratio of the numbers of more or less specialist and generalist species, however, not by the size of the difference between the most specialized and most ubiquitous species.

4.3.4 Sites and periods

In further groups of scenarios, the range of the habitat axis covered by the sites was varied. Using the sites as samples, the increasing habitat range made the distributions of species' recording frequencies less bimodal (Fig. 27). Using the periods as samples, there was a small but opposite effect (Fig. 27). As the habitat range in the simulation represented differences of the habitat inside study sites, it was clearly a spatial kind of heterogeneity. Thus, it mainly affected the distributions of species' recording frequencies when using the sites as samples. Using the periods as samples, the more a

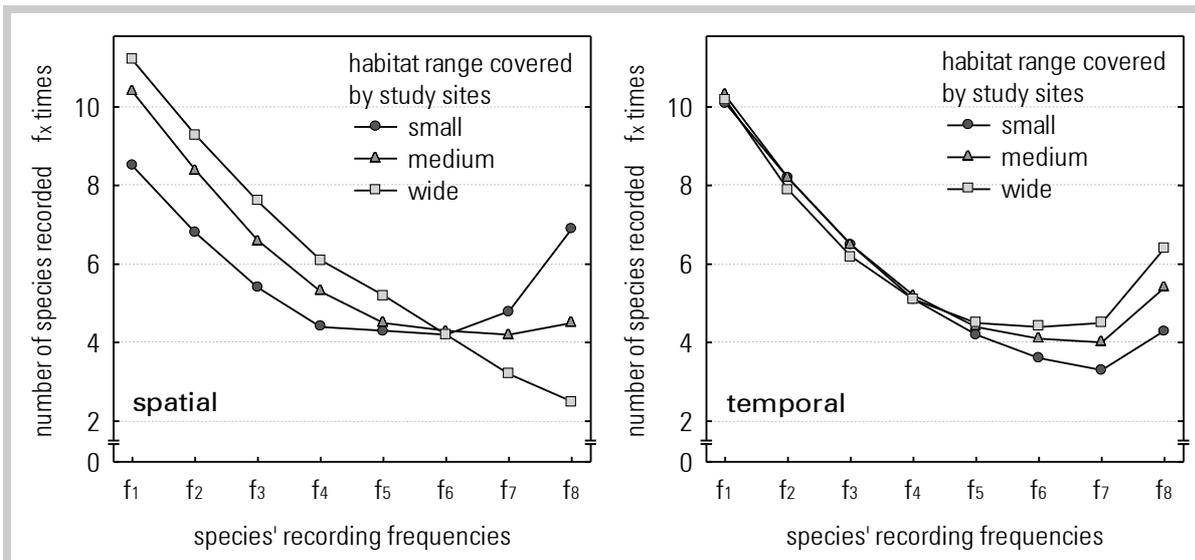


Fig. 27 Effect of habitat range covered by the sites on the curve shape of the distribution of recording frequencies.

habitat gradient was covered by a site, the more species' niche ranges were covered by this site. Thus, depending on whether the samples were used spatially or temporally, the same source of heterogeneity affected the distributions of species' recording frequencies in different ways. This became more obvious with the CSI. Whereas for spatial use, the CSI decreased when the habitat range of the sites became wider, for temporal use, the CSI increased slightly (Fig. 28).

The CSI values of groups of scenarios are shown for comparison, in which the range of the habitat axis, that was covered by the traps inside the sites was varied. The CSI remained almost unchanged, when the ranges of the sites increased, in which the traps were situated (Fig. 28). The five traps of one site covered quite small ranges of the habitat gradient compared to the range covered by all the sites. Thus, increasing the width of the sites and, hence, the range of possible trap positions, introduced comparably very little heterogeneity, which hardly affected the distribution of the recording frequencies.

Two groups of scenarios, one with an increasing variability in the effectiveness of the traps for all species and one additionally with sites and traps covering increasing ranges of the habitat axis were compared. By increasing the variation in the effectiveness of the traps only, the CSI increased in the spatial as well as in the temporal sampling (Fig. 29). On the other hand, combining the different kinds of heterogeneity as in the second group of scenarios, the

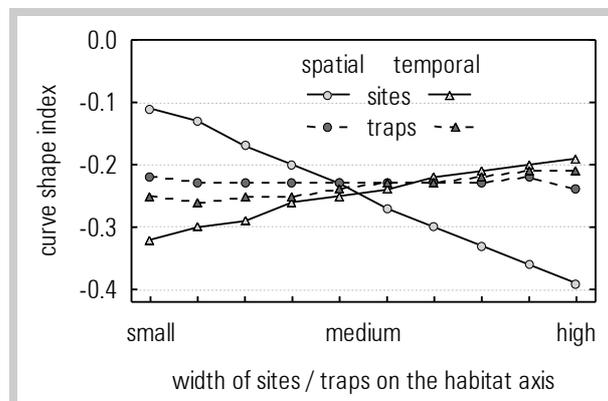


Fig. 28 Effect of habitat ranges covered by sites and by traps inside the sites respectively on the CSI.

CSI decreased with an increasing combined spatial heterogeneity, when using the sites as samples. However, the CSI increased, when using the periods as samples (Fig. 29). Generally, a higher variation of the effectiveness of traps resulted in higher species' recording probabilities in some of the traps and, hence, for the sites and periods. Thus, the effect of the range of habitat axis covered by the sites (and traps) as shown in Figure 28, was clearly altered by the differences in the variation of the traps' effectiveness.

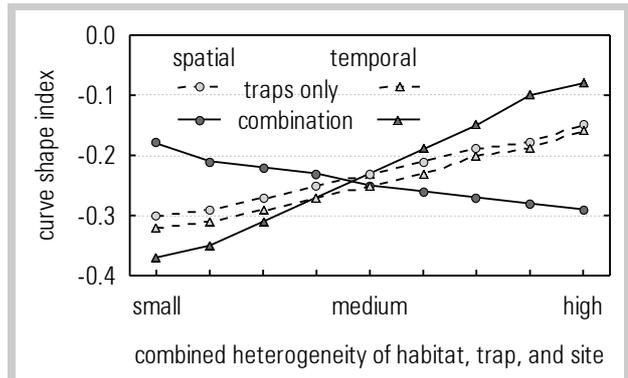


Fig. 29 Effect of increasingly variable effectiveness of traps on the CSI and modified by the effect of the increasing sites' habitat range.

Temporal heterogeneity was implemented in the simulation in two ways, with equal differences in the recording probability per period for all species and alternatively with the species being differently affected by the conditions of the periods. This was compared in two groups of scenarios.

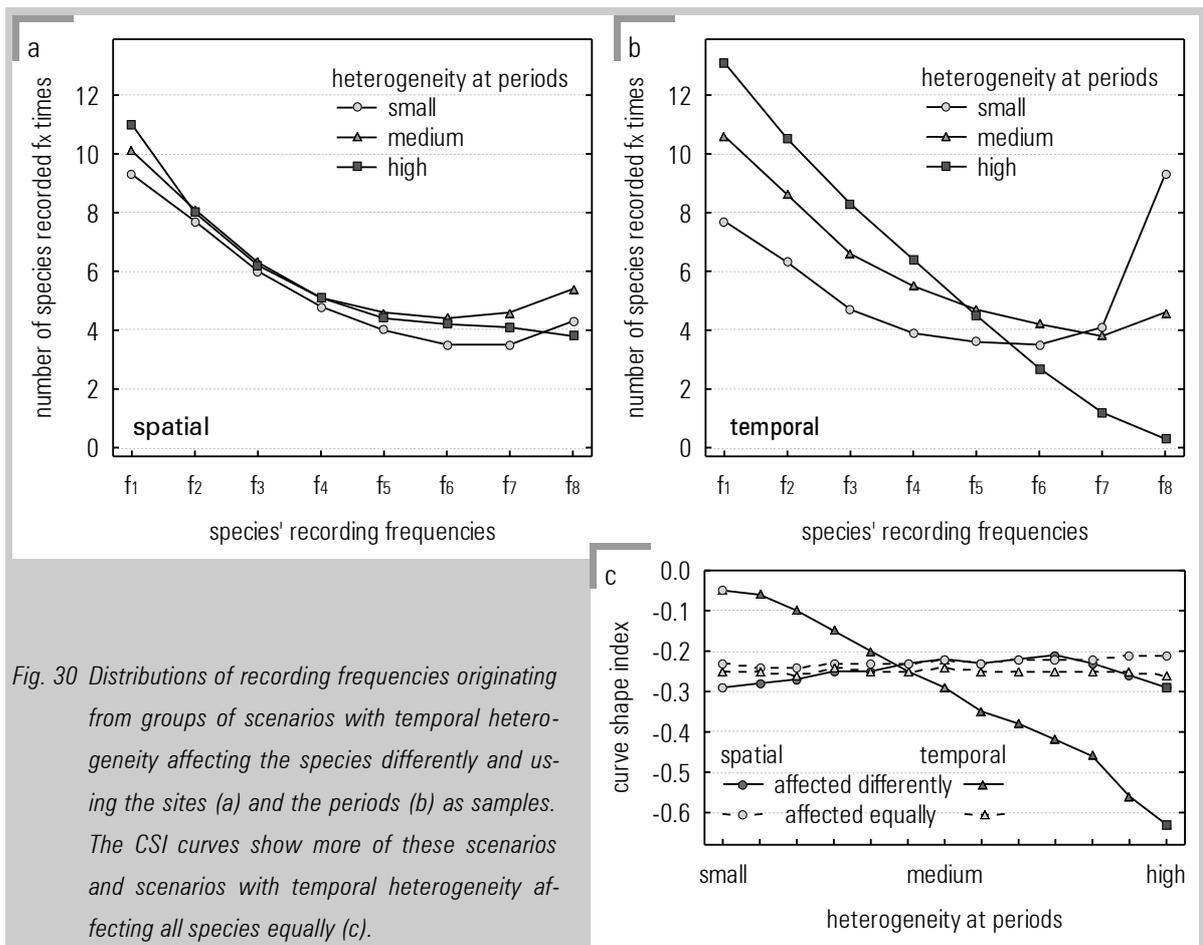


Fig. 30 Distributions of recording frequencies originating from groups of scenarios with temporal heterogeneity affecting the species differently and using the sites (a) and the periods (b) as samples. The CSI curves show more of these scenarios and scenarios with temporal heterogeneity affecting all species equally (c).

In the latter case, using the species records as samples of periods, the distributions of the recording frequencies became more bimodal and the CSI decreased rapidly with increasing heterogeneity (Fig. 30b,c). However, taking the sites as samples, the effect of increasing temporal heterogeneity on the distributions of the recording frequencies and on the CSI was small (Fig. 30a,c). This means, that not only the curve shapes were very similar but the temporal heterogeneity did not affect the spatial samples. In the temporal case, the curve shapes changed drastically with increasing heterogeneity (Fig. 30a,b). Thus, it can be concluded that also in scenarios with temporal heterogeneity, the use of the data (sites or periods as samples) mainly determine the effect of heterogeneity.

On the other hand, there was hardly an effect, when temporal heterogeneity increased the recording probability for all species in "good" periods and decreased it in "bad" periods (Fig. 30c). Moreover, it made no difference, whether the species records were used temporally or spatially (Fig. 30c). Thus, these scenarios showed, that differences between periods are a clearly stronger source of temporal heterogeneity when they affect the species differently.

4.3.5 Combined sources of heterogeneity in samples

Two groups of scenarios were chosen to show the complex effects of different sources of heterogeneity on the distribution of species' recording frequencies and on the CSI. The scenarios with isolated sources of heterogeneity in the simulation showed that some of them have parallel and others contrary effects on the CSI. For the first group of scenarios, the maximum and minimum niche width and the range on the habitat axis covered by the sites and traps were chosen, because they simultaneously increased the CSI when increased (combination 1). The second group of scenarios is based on differences among periods and among the species reactions on temporal differences as well as the range on the habitat axis covered by sites and traps and the effectiveness in recording sites and traps (combination 2). Increasing them lead to divergent effects on the CSI.

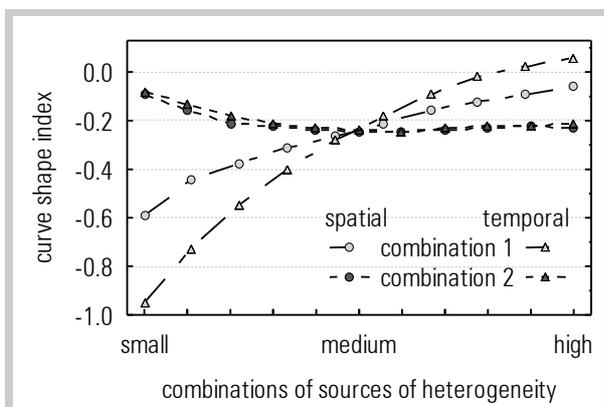


Fig. 31 Effect of combinations of different sources of heterogeneity on the CSI.

For spatial sampling and so even more for temporal sampling, the CSI increased drastically (Fig. 31) with combination 1. These factors complement one another because the increasing number of ubiquitous species compensates for the effect of the increasing differences of the sites. For combination 2, the CSI was high and changed only slightly (Fig. 31). Thus, the effect of the increasing heterogeneity was balanced and very similar for both, the temporal and the spatial sampling. These scenarios

showed that it is difficult to predict the effect on the distribution of species' recording frequencies, even if the acting factors and their values, as in a simulation, are known.

4.3.6 Species number

The effect of the number of species on the distribution of species' recording frequencies and the CSI was studied with a group of scenarios varying the species number only. The species number itself obviously did not affect the CSI (Fig. 32) for both, the spatial and the temporal way of sampling.

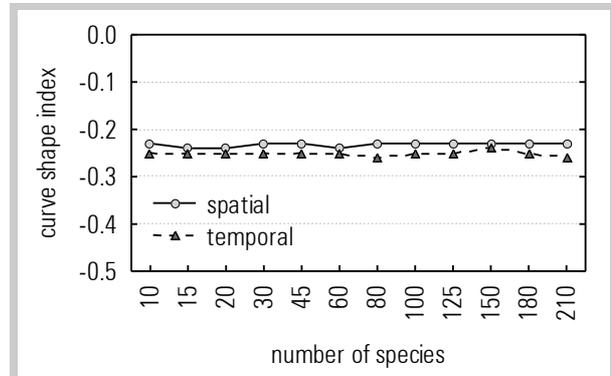


Fig. 32 Effect of different species numbers on the CSI.

4.3.7 Number of species records and heterogeneity

The total number (of incidences) of species records (Ncap) of a simulated sample depends on the effort and on the number of species (60 in this simulation), in particular because the recording probability of each single species in the simulation is independent of the number of species. However, heterogeneity in the spatial and temporal samples affected the number of species records.

In a group of scenarios the range in which the sites can be found on the habitat axis was varied. The remaining parameters of the simulation took the default values (Tab. 3). The number of species records increased with increasing heterogeneity in the temporal case, but decreased in the spatial case (Fig. 33). The wider the range on the habitat axis over which sites were placed, the more ranges of high recording probability of different species were covered and the more different the species communities recorded on the sites. Thus, the number of sites on which quite abundant species could be regularly recorded decreased because the sites became less similar. Nevertheless, some species were

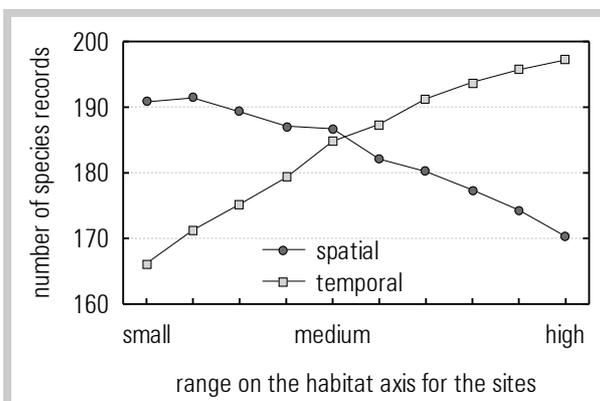


Fig. 33 Effect of habitat width on the number of species records for spatial versus temporal sampling.

abundant enough to be recorded over every period and the wider habitat range of the sites covered the range of highest recording probability of an increased number of species. Thus, the numbers of species records increased with the increasing heterogeneity when sampling temporally, however, not when sampling spatially.

Groups of scenarios with increasing numbers of periods showed the effect of increasing effort and simultaneously increasing temporal heterogeneity on the number of species records

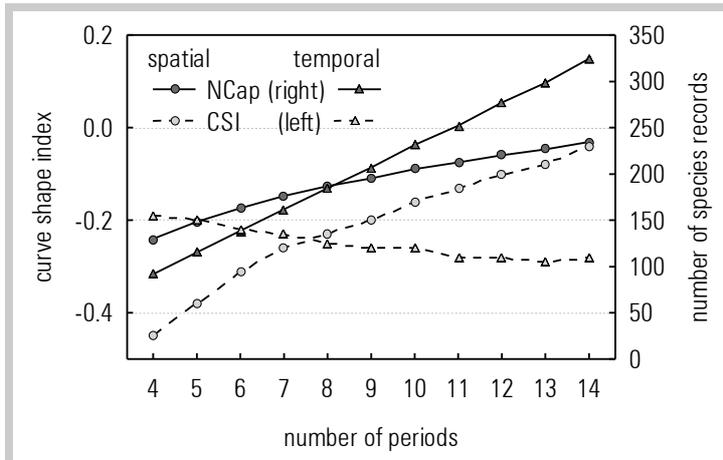


Fig. 34 Effect of increasing effort on the number of species records and the CSI.

(Ncap) and the CSI. Using the samples spatially, the number of species records and the CSI both increased with increasing effort (Fig. 34). Using the samples temporally, the number of species records increased with the increasing effort whereas the CSI decreased. In groups of scenarios shown above (Fig. 22) the effect of the increasing effort on the CSI was counterbalanced by the increasing temporal heterogeneity introduced by

additional periods. This heterogeneity also affected the number of species records but not that strongly. Thus, the number of species records increased with the number of periods both temporally as well as spatially. From this it can be concluded that the number of species records and the CSI can be differently affected by factors, which modify the recording probabilities of species.

4.4 Discussion

4.4.1 Factors affecting the distributions of recording frequencies

As effort greatly affects the probability of species being recorded, it was not surprising that it was the main factor changing the curve shape of the distribution of species' recording frequencies. When sampling with low effort, the distribution of species' recording frequencies was usually unimodal and most of the species were rarely recorded. When sampling with high effort, the distribution was often bimodal sometimes with a majority of the species being recorded regularly (compare Chapter 3.3.2). However, the differences in sites and periods combined with species characteristics could counterbalance the effect of the effort.

The two factors of niche width determine in the simulation, to which extent a species community is characterized by generalist or specialist species. The higher the ratio of generalists was, the more bimodal was the distribution of the recording frequencies. However, this distribution was not affected by the range of the niche width between the most specialized and most ubiquitous species.

Sites and traps can cover different ranges of a habitat gradient and can vary in their effectiveness in recording species. When increasing the habitat range of the sites, the CSI was clearly affected, whereas increasing that of the traps hardly affected the CSI. In contrast, when increasing the variability of the traps' effectiveness, the CSI was affected, whereas increasing that of the sites, it was not. Conse-

quently, these two sources of spatial heterogeneity affect the distributions of recording frequencies in a different way.

Sampling periods can generally differ in the recording probability for all species or the different conditions of the periods can differently affect the species in their recording probability. Whereas the first source of temporal heterogeneity hardly affected the CSI, the second clearly did.

The number of species of a community never had an effect on the distributions of species' recording frequencies and, hence, on the CSI.

The general rule from the simulation is that increasing effort leads to increasing numbers of regularly recorded species, whereas some kind of heterogeneity leads to increasing numbers of rarely recorded species. However there are exceptions. The most important of them is discussed in the following paragraph.

There was no general difference between sampling spatially, using sites as samples, and temporally, using periods as samples. However, sources of heterogeneity, which were spatial or temporal, affected these two ways of sampling differently. When the differences between the sites increased, a smaller ratio of the species appeared on many of the sites and, hence, in many of the spatial samples. Thus, the number of regularly recorded species decreased. On the other hand, all the species from the different sites had an equal chance of appearing over each of the periods in the temporal samples. Thus, species, which were abundant at only one of the sites could be recorded quite regularly in the temporal samples. Therefore, increasing spatial heterogeneity decreases the CSI when sampling spatially and increases the CSI when sampling temporally. With temporal heterogeneity, it is the other way round.

In general, the CSI and the number of species records jointly increased and decreased in the simulation. The CSI and the number of species records are similar in some respects, because the distribution of species' recording frequencies is built up by these species records. Moreover, they regularly reacted in a similar way to the factors of heterogeneity. Increasing the spatial heterogeneity, the number of species records, too, increased in temporal sampling, however, decreased in spatial sampling. In case of temporal heterogeneity it is the other way round. On the other hand, groups of simulation scenarios with increasing effort and consequently increasing heterogeneity had a different effect on CSI and the number of species records. Whereas the temporal heterogeneity, which is connected to the increasing effort in these groups of scenarios, was strong enough to change an increasing CSI in the spatial sampling to a decreasing CSI in the temporal sampling, the steep increase in the number of species records in the temporal sampling was hardly flattened in the spatial. Thus, it can be concluded that in a complex system of factors the number of recorded species and the CSI are almost unrelated.

4.4.2 *Comparison with experience from the field*

Even if some of the ranges set in the simulation for heterogeneity or other factors may have been unrealistic, the resulting distributions of recording frequencies were realistic since all types of distributions observed in the simulations were also found in the field data (see Chapter 3.3). Moreover, some of the ranges used in the simulations for factors like effort and variance of the general recording probabilities of periods and sites are known from the field data of this and other studies (CODDINGTON ET AL. 1996).

In the field it is usually difficult to increase effort without getting additional heterogeneity. Whereas the extent of the effort is obvious, the resulting change in heterogeneity is difficult to detect. Thus, in field data it is unclear, how far the effect of effort on distributions of species' recording frequencies is balanced by the effect of heterogeneity. Joining the results of the simulation and of the field data (Chapter 3.3), the effort showed to be the strongest factor affecting the CSI and the number of species records.

The strong differences in the number of recorded species as well as in the number of captured individuals between sampling periods indicate general differences of capture probabilities among periods (see Chapter 3.3.4) in the field data. Weather factors can explain this because they correlated with these differences. However, the simulation showed that such strong effects on the CSI can only be explained by assuming that the species individually react to the differences in the periods. Thus, the effect of temporal heterogeneity on the distributions of the species' recording frequencies in the field data most probably originates from individual reactions of the species on changing conditions among the trapping periods.

In field studies, which aim to estimate local species richness, it has to be decided whether to perform a spatial or temporal sampling design. This decision is usually based on a number of prerequisites, for example the species community has to be closed over the study period, thus, it can not last very long, or the availability of trapping sites within a habitat is limited. Provided that the heterogeneity of sites and periods is similar, the results of the simulation showed no a priori advantage from one of the two designs.

4.4.3 *Modeling recording frequencies to study species richness estimators*

The incentive to study the distributions of species' recording frequencies and the number of species records is that they are the base of information for species richness estimators using mark-recapture like data (BURNHAM & OVERTON 1978, CHAO 1984, CHAO ET AL. 1992, OTIS ET AL. 1978). Thus, a simulation aiming to study the factors affecting the accuracy of species richness estimators must find a way to model the effect of these factors on the parameters, on which the species richness estimators are based.

In the statistically similar situation of estimating species abundances when capture probabilities of individuals are heterogeneous, the beta distribution was used to model the distribution of capture frequencies (CHAO 1987, CHAO 2001, BURNHAM & OVERTON 1979). However, using such a distribution of recording frequencies for species richness estimation fixes the unknown effects of spatial and temporal heterogeneity of the samples and of species characteristics like habitat use instead of modeling them. Thus, in this study a very simple habitat model has been developed to investigate the effect of these factors on the curve shape of the distribution of species' recording frequencies and the numbers of species records.

First, a rough assumption about the range of the recording probabilities of the species is required for the simulation. Species' abundance distributions can be assumed to be a reflection of the underlying relative probabilities of the species being detected. Species abundances have been found to cover a range of about eight octaves (CODDINGTON ET AL. 1996) and be exponentially distributed (ENGEN & LANDE 1996). Thus, the distribution of the species recording probabilities underlying the simulation can be expressed as the density function of the exponential distribution ($f(x) = e^{-x}$). Using $x = 4.7$ as the standard value for the simulation was selected based on a comparison of simulated distributions for different values of x with distributions of species' recording frequencies from field data. Moreover, this value for x is reasonable because it produces a range of about eight octaves of species abundances, which was also reported by CODDINGTON ET AL. (1996).

As the set of recording frequencies is one of the basic parameters of species richness estimators, which are related to mark-recapture approaches, the ratio of rarely recorded species and regularly recorded species may serve to evaluate the estimators. Looking for a parameter, which expresses, how far the curve is unimodal (many rarely recorded species) or bimodal (at least a few regularly recorded species), the curve shape index (CSI) was developed. The simulations showed that the different sources of heterogeneity and species characteristics have complex effects on the distributions of species' recording frequencies. Thus, the CSI can be expected to be a useful tool to express the curve shapes of these distributions in one number and, hence, to compare the influence of these frequency distributions on the accuracy and reliability of species richness estimators.

In summary, the simulated distributions of species' recording frequencies and numbers of species records as well as their comparison to distributions from the field showed that the way of modeling in this simulation provides useful and plausible results. Thus, this simulation using the CSI and the number of species records as parameters is a good basis from which the accuracy and reliability of species richness estimators can be studied.

5 Accuracy and reliability of species richness estimators in simulation

5.1 Introduction

The number of species of an area or a species community is a basic parameter of biodiversity (NICHOLS ET AL. 1998B). Even for immobile species and in small areas it is usually not achievable to record all species present. Thus, a number of methods have been implemented to estimate species richness from samples of incomplete inventories (BUNGE & FITZPATRICK 1993). COLWELL & CODDINGTON (1994) divided the concepts of these methods into three groups: extrapolating species accumulation curves, fitting parametric models of relative abundance, and nonparametric methods (see Chapter 1.2). Some of these methods of estimating species richness were compared based on the biological plausibility of the results from different estimators (e.g. WALTHER & MARTIN 2001) and seemed to work more or less satisfactorily.

The concept of this study has been to test the suitability of some mark-recapture methods, which were originally developed to estimate population sizes, for species richness estimation. The species of a community definitely do not have equal probabilities of being recorded (BOULINIER ET AL. 1998). Moreover, the samples of species inventories are usually taken from sites and over periods, which are more or less heterogeneous in terms of their general recording probabilities of the species (HINES ET AL. 1999). Thus, in terms of mark-recapture methods, model M_h or M_{th} estimators (see Chapter 3.3.4) have to be chosen (BOULINIER ET AL. 1998). This study is focused on nonparametric methods of species richness estimation, which were originally developed for estimating abundances. Most of the species richness estimators selected or at least their concept of estimating species richness have been used before (COLWELL & CODDINGTON 1994, WALTHER & MARTIN 2001). However, the concept of the simulation used to test them in this study is innovative.

The "true" number of species of a community from the field is never known. Thus, the accuracy and reliability of the estimates can only be conjectured. Former concepts of modeling heterogeneous recording probabilities in simulations can be divided into two groups. Those of the first group are based on distributions of species abundances in which differences between the distributions reflect different degrees of heterogeneity (HELTSHE & FORRESTER 1983, BALTANÁS 1992, KEATING ET AL. 1998, CHAO & BUNGE 2002). Those of the other group are based on recording probabilities of the species and heterogeneity is introduced via a number of discrete recording probabilities for a number of groups of the species or a distribution of species' recording probabilities (CHAO & LEE 1990, CHAO & LEE 1992, CHAO ET AL. 1996, CHAO ET AL. 2000). In both groups the sources of heterogeneity of spatial or temporal samples with their more or less opposite effects on the recording probabilities of the species (see Chapter 3.3 and 4.3) are reflected in one distribution. Thus the factors introducing heterogeneity cannot be separately studied in such simulations.

The alternative used in this study is to vary those factors in a simulation which proved to introduce heterogeneity in field data. The distribution of species' recording frequencies, the number of species recorded once (f_1) twice (f_2) and so on, are the condensed recording history of a studied species community. As the studied species richness estimators are based on at least f_1 (BURNHAM & OVERTON 1978), f_1 and f_2 (BURNHAM & OVERTON 1978, CHAO 1984), or more of the recording frequencies (CHAO ET AL. 1992) and the number of species records (CHAO ET AL. 1992, OTIS ET AL. 1978), the curve shape of the distribution of species recording frequencies can be used to evaluate whether the settings of the simulation are realistic. This way, the advantage of the simulation, knowing the "true" number of species, can be combined with the knowledge from the field about the effects of different sources of heterogeneity in the samples on the distributions of species' recording frequencies (see Chapter 3.4.2). Thus, the effects of this heterogeneity on the accuracy and reliability of the species richness estimates of different methods can be studied.

It can be assumed that the accuracy and reliability of each species richness estimation is affected by the effort, by characteristics of the species, like the species number and choice of the habitats, and by differences among the sampling sites and sampling periods. Most of these factors have unknown values in field data (see Chapter 3.3). However, four factors can be extracted from the field data, which summarize the effects of all those factors and which are used in species richness estimators. It is the number of recorded species (D), the number (of incidences) of species records (N_{cap}), a quotient of them (N_{cap}/D) and the distribution of species' recording frequencies, expressed as an index (CSI) (see Chapter 4.2.3). As these are probably correlated, these correlations must be detected first.

Because of their different underlying concepts, it can be conjectured that the estimators do not work equally well depending on the ranges of the factors like effort, species' characteristics and heterogeneity of samples. The aim of this study is to find out using a simulation which of these estimators yield the most accurate and reliable estimates of species richness under which conditions and, hence, can be recommended under definite conditions. In order to define these conditions the curve shape of the distribution of species' recording frequencies expressed as CSI and the number of species records shall be utilized to propose useful criteria.

5.2 Methods

5.2.1 Parameters to predict the performance of the estimators

One aim of this study is finding parameters to predict which of the species richness estimators will perform best with a given data set from the field. Useful parameters must be assumed to affect the performance of the estimators and must be able to be derived from field data. As the number of recorded species (D), the number (of incidences) of species records (N_{cap}), a quotient of them

(Ncap/D) and the distribution of species' recording frequencies, described as CSI (see Chapter 4.2.3 and 4.4) meet these conditions, they can be used as criteria to choose the best estimator for a definite data set. Since these parameters are more or less correlated, it is not useful to apply all of them to analyze and to predict the performance of the estimators of species numbers.

In order to select the important parameters, a principal component analysis (PCA) was carried out with the commercial statistic software STATISTICA (STATSOFT 2001). It was based on the nine groups of simulation scenarios which were used to study the effects of effort. These were chosen because they offered a wide range of the values from the studied parameters. From each of these nine groups of scenarios one spatial and one temporal sample of values of the number of recorded species (D), the number of species records (Ncap), a quotient of them (Ncap/D) and the distribution of species' recording frequencies, described as CSI was taken by simple random sampling with replacement. This way, 20 datasets with 18 values of these four parameters each were created to be analyzed with a PCA. The results of the PCA of these different data sets were compared looking for a common pattern of the relative importance of the aforementioned parameters.

5.2.2 Notation

\hat{N}	= estimate of the number of species N
\hat{C}	= estimate of the sample coverage C
t	= number of samples from sampling sites or periods
D	= number of distinct species recorded in t samples = $\sum_{i=1}^t f_i$
f_i	= number of species recorded exactly i times in t samples
n_j	= number of species recorded in the j th sample
$\sum_{i=1}^t if_i$	= number (of incidences) of species records in t samples
\hat{y}^2	= estimated square of the coefficient of variation

5.2.3 Estimators

The following ten estimators were chosen to be studied by simulation. All the equations are presented in detail in the Appendix. The estimators can be divided into four groups with different statistical concepts, the coverage estimators, the moment estimator, the jackknife estimators, and the maximum likelihood estimator. The presentation starts with estimators, which are based on the concept of coverage.

The presentation starts with two estimators of the jackknife-type (BURNHAM & OVERTON 1978, BURNHAM & OVERTON 1979). Originally, the jackknife procedure was a bias reduction technique. The basic idea of the

jackknife is to reduce the bias of an estimator by taking advantage of subsamples drawn from the entire sample. In this case, the recorded number of species serves as an initial biased estimator and it is assumed that this bias can be formulated as a series of $1/t$. Applying this concept to species records the first order jackknife, *Jackknife1* (J1) results.

$$\hat{N}_{J1} = \sum_{i=1}^t f_i + \left(\frac{t-1}{t}\right) * f_1$$

Very similar to this is the second order jackknife *Jackknife2* (J2), which adds a second step of bias correction.

$$\hat{N}_{J2} = \sum_{i=1}^t f_i + \left(\frac{t-1}{t}\right) * f_1 - \left(\frac{(t-2)^2}{t * (t-1)}\right) * f_2$$

The second group consists of estimators, which are based on the concept of coverage. Let p_1, p_2, \dots, p_N be the recording probabilities of the N species in the studied community. The coverage of a sample quantifies the proportion of relative abundances which is represented in the sample.

$$C = \frac{\sum_{\text{all species} \in \text{the sample}} p_i}{\sum_{i=1}^N p_i} = \sum_{\text{all species} \in \text{the sample}} p_i$$

Since neither N nor the recordability of the species p_i are known, C can only be estimated from the sample. It turns out (CHAO ET AL. 1992) that the recording frequencies f_i of the species provide a basis for reasonable estimates of C . CHAO derived three different estimators of C :

$$\hat{C}_1 = 1 - \frac{f_1}{\sum_{i=1}^t i f_i}, \quad \hat{C}_2 = 1 - \frac{f_1 - \frac{2f_2}{t-1}}{\sum_{i=1}^t i f_i}, \quad \hat{C}_3 = 1 - \frac{f_1 - \frac{2f_2}{t-1} + \frac{6f_3}{(t-1)*(t-2)}}{\sum_{i=1}^t i f_i}$$

In the simplest case of all p_i -s being equal the coverage equals the proportion of species recorded, $C = D/N$, and a natural estimator \hat{N} of the total species number is given by:

In the more general case of varying recordabilities of species, the degree of heterogeneity of these recordabilities, measured as the coefficient of variation γ , has to be incorporated into a suitable estimator of species number. This square of the coefficient of variation again has to be estimated and different proposed estimators are:

$$\hat{\gamma}_1^2 = \max \left[\frac{\sum_{i=1}^t f_i}{C} * \frac{\sum_{i=1}^t i(i-1)f_i}{2 \sum_{i < j} \sum_{j=1}^t n_i n_j} - 1; 0 \right] \quad \hat{\gamma}_4^2 = \max \left[\frac{\sum_{i=1}^t f_i}{C} * \frac{\sum_{i=1}^t i(i-1)f_i}{\sum_{i=1}^t i f_i * \left(\sum_{i=1}^t i f_i - 1\right)} - 1; 0 \right]$$

Tab. 4 Combinations of estimators of \hat{C} and \hat{y}^2 used in the simulation.

Cover1	\hat{C}_1	\hat{y}_1^2	(CHAO ET AL. 1992)
Cover2	\hat{C}_2	\hat{y}_1^2	(CHAO ET AL. 1992)
Cover3	\hat{C}_3	\hat{y}_1^2	(CHAO ET AL. 1992)
Cover4	\hat{C}_1	\hat{y}_4^2	(CHAO & LEE 1992)
Cover5	\hat{C}_1	\hat{y}_5^2	(CHAO & LEE 1992)
Cover6	\hat{C}_1	\hat{y}_6^2	(CHAO & LEE 1993)

$$\hat{y}_5^2 = \max \left[\hat{y}_1^2 * \left(1 + \frac{f_1 * \sum_{i=1}^t i(i-1)f_i}{\sum_{i=1}^t if_i * \left(\sum_{i=1}^t if_i - 1 \right) * \hat{C}} \right); 0 \right]$$

$$\hat{y}_6^2 = \max \left[\frac{\sum_{i=1}^t f_i}{C} * \frac{\sum_{i=1}^t i(i-1)f_i}{\left(\sum_{i=1}^t if_i \right)^2} - 1; 0 \right]$$

The general form of the coverage estimator of species number in the case of varying recording probabilities is

$$\hat{N} = \frac{\sum_{i=1}^t f_i}{C} + \frac{f_1}{C} * \hat{y}^2$$

where different combinations of estimators for \hat{C} and \hat{y}^2 result in different versions of coverage estimators (Tab. 4).

The third group of estimators has only one member, in the study called *Moment* (CHAO 1984, CHAO 1987, CHAO 1988). The idea is to simply use a proportion of the species recorded once and those recorded twice as a measure of the difference between the recorded number of species and the "true" number of species, which has to be estimated. Thus, it has the disadvantage of returning no result if $f_2 = 0$. This particularly occurs, when species numbers are small and capture probabilities are high enough to record many of the species regularly.

$$\hat{N} = \sum_{i=1}^t f_i + \frac{f_1^2}{2f_2}$$

The maximum likelihood estimator *MaxLike* (OTIS ET AL. 1978) (the only member of the fourth group) was developed for equal recording probabilities and, hence, has been included in this study mainly for reasons of comparison. Maximum likelihood estimation begins with writing a mathematical expression known as the Likelihood Function of the sample data, in this case the species records. The likelihood of a set of data is the probability of obtaining that particular set of data, given the chosen model of equal recording probability in this case. This expression contains the unknown model parameter N . The value \hat{N} that maximize the sample likelihood is the Maximum Likelihood Estimate \hat{N} .

$$\hat{N} = N \text{ with } \max[\ln L]$$

More details of the calculation of the estimators can be found in the Appendix. In addition, formulas for variance estimation are provided in the Appendix for all estimators studied in this simulation.

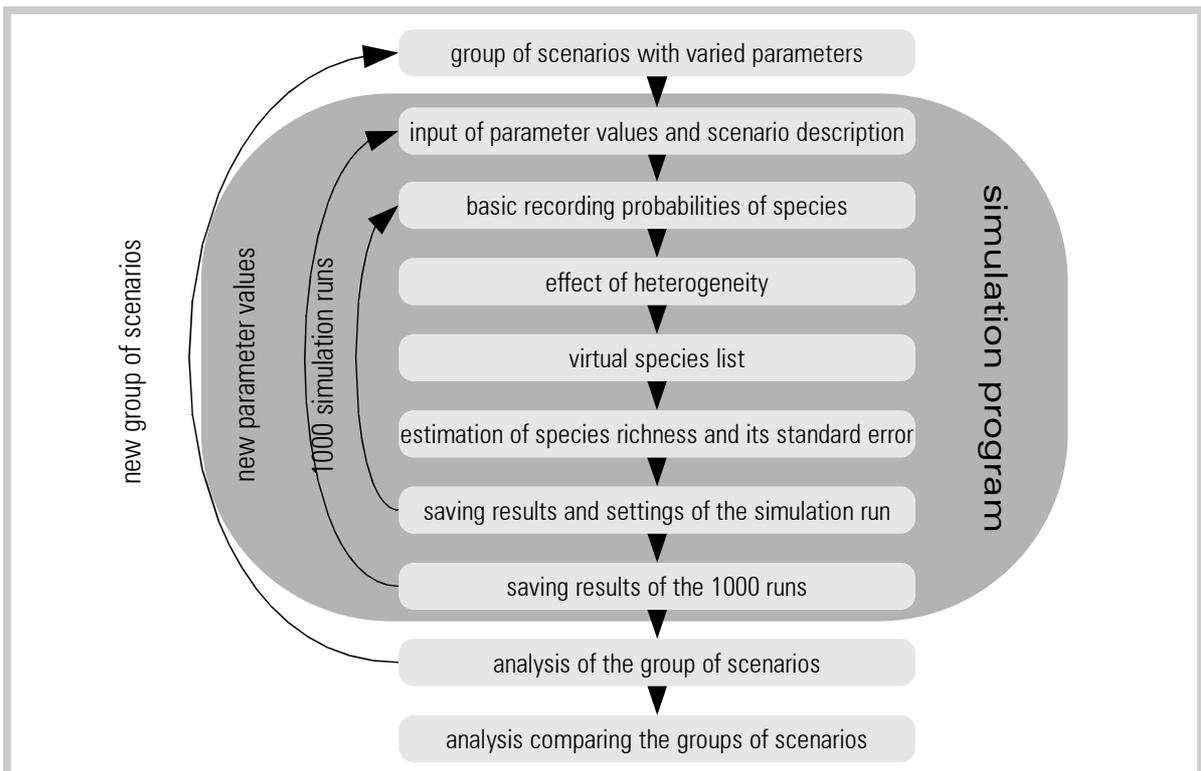


Fig. 35 Structure of the simulation used to study the performance of the species richness estimators.

5.2.4 Simulation

The simulation was performed with scenarios of effort and of different kinds of heterogeneity originating from species characteristics and from differences of the sampled sites and periods. In each group of scenarios one factor or a combination of some of these is studied with changing values. For each of the scenarios 1000 simulation runs were performed (Fig. 35) with random differences which were limited by the scenario and its values of the factors. Details of simulating differences in effort, spatial and temporal heterogeneity of the samples, and species' characteristics, can be found in Chapter 4.2.1 and 4.2.2.

5.2.5 Evaluation of the estimators

Within this study the performance of the different estimators is evaluated using three parameters, the mean percentage difference between the estimated and the "true" number of species, the percentage of bias and the standard error of the estimates.

$$\text{mean percentage difference} = \frac{1}{n} \sum_{i=1}^n \frac{|N_{true} - N_{est}|}{N_{true}} * 100$$

The mean percentage difference is calculated by dividing the absolute value of the difference of the estimated number of species N_{est} and the "true" number of species N_{true} by the "true" number of

species. Then the mean of these differences of the simulation runs with a definite set of parameter values from the simulation is calculated using the number of simulation runs n , which was always 1000 in this study.

$$\text{percentage bias} = \frac{1}{n} \sum_{i=1}^n \frac{N_{true} - N_{est}}{N_{true}} * 100$$

The percentage bias is calculated very similarly, however, using the difference instead of the absolute difference of the estimated number of species from the “true” number of species. Hence, the percentage bias reflects how far an estimator consistently over- or underestimates the “true” number of species. An unbiased estimator is not necessarily an accurate estimator. If an estimator is sometimes much too high and sometimes much too low, it can still be unbiased. Nevertheless, it would be very inaccurate. A slightly biased estimator that systematically results in very small overestimates of a parameter could be quite efficient. Thus, mean percentage difference and percentage bias are both necessary to evaluate the performance of the species richness estimators.

$$\text{standard error of the estimates} = \sqrt{\frac{1}{n} \sum_{i=1}^n (N_{est} - \bar{N}_{est})^2}$$

The standard error of the species richness estimates is the standard deviation of the sampling distribution of the species richness estimation. The standard deviation describes the variability of a group of species richness estimates by evaluating how they differ from the average, however, not from the “true” number of species. In order to analyze some of the estimators in detail, contour plots were used, which were based on all simulations dealing with the different sources of heterogeneity and effort. The distributions of the contour levels were calculated with the distance weighted least square method. The same species records can result in different distributions of recording frequencies depending on whether they are used in a spatial or temporal direction. The differences become more explicit the more the sources of heterogeneity affect either only the periods or the sites. Thus, each simulation run was simultaneously analyzed spatially and temporally.

To keep track of the relative performance of the estimators in different situations, a system of ranking was used. In a first step the estimators were ranked for every scenario by their mean percentage difference, by their percentage bias, and by the standard error of 1000 simulation runs. This makes it easy to analyze how the estimators change in performance when parameter values of the simulation scenarios change. However, the ranks of the estimators can be quite different for mean percentage difference, percentage bias or standard error. Therefore, these three rankings were combined by calculating a weighted mean rank.

The mean percentage difference was weighted highest (weight: 5) because it reflects the probability of the estimation result to meet the “true” number of species. The percentage bias was weighted less (weight: 3) because an estimator with a small percentage bias but a high mean percentage dif-

ference is not reliable, even if it meets the “true” number of species on average. The standard error was weighted least (weight: 2), because even a heavily biased estimator can show a small standard error and it is also a measure for reliability as the mean percentage difference. For the ranking, the standard error of the simulation runs was used to compare species richness estimators, because the estimators of variance, provided by the species richness estimators are not comparable.

For all groups of scenarios varying one or more parameters of the simulation, the ranking was performed in a similar way. First, the median of the ranks of the simulation runs was calculated separately for the mean percentage difference, percentage bias and standard error. Then the weighted mean ranks for the estimators were calculated for the single scenarios. This ranking gives an overview of which of the estimators is robust against the different sources of heterogeneity.

5.3 Results

The condensed result of the simulation was that *Jackknife1*, *Cover1*, and in some situations *Jackknife2* are the most accurate and reliable estimators of species richness in this study and that the number of species records and the curve shape index (CSI) are useful to predict the best estimator for a definite data set. These results are based on ranks of the estimators in all simulated scenarios. However, in order to clarify the factors leading to the differences in the performance of the estimators, the most instructive groups of scenarios of the simulation were selected.

First, it was shown, that two parameters used in the estimators, the CSI and the number of species records, sufficiently represent factors affecting the performance of the estimators (Chapter 5.3.1). The relative performance of the estimators was affected by factors like effort and heterogeneity of the samples shown by the parameters CSI and number of species records (Chapter 5.3.2). This is illustrated by selected groups of scenarios. Thereafter a detailed comparison of some of the estimators follows with some more instructive groups of scenarios. These comparisons showed that either *Jackknife1* or *Cover1* or *Jackknife2* (Chapter 5.3.3) can perform best depending on the values of the CSI and the number of species records. The ranking condensed these results to a comprehensive picture of the performance of the species richness estimators and provided general rules as to when to use which of them (Chapter 5.3.4).

5.3.1 Useful parameters for comparison

The principal component analysis of the relations between the number of recorded species (D), the number of species records (N_{cap}), a quotient of them (N_{cap}/D), and the distribution of species' recording frequencies, described as CSI, displayed a common pattern. A typical example of this pattern is given in Figure 36a. The number of recorded species (D), the number of species records (N_{cap}), and a quotient of them (N_{cap}/D) were oriented mainly parallel to the axis of the first factor. The CSI

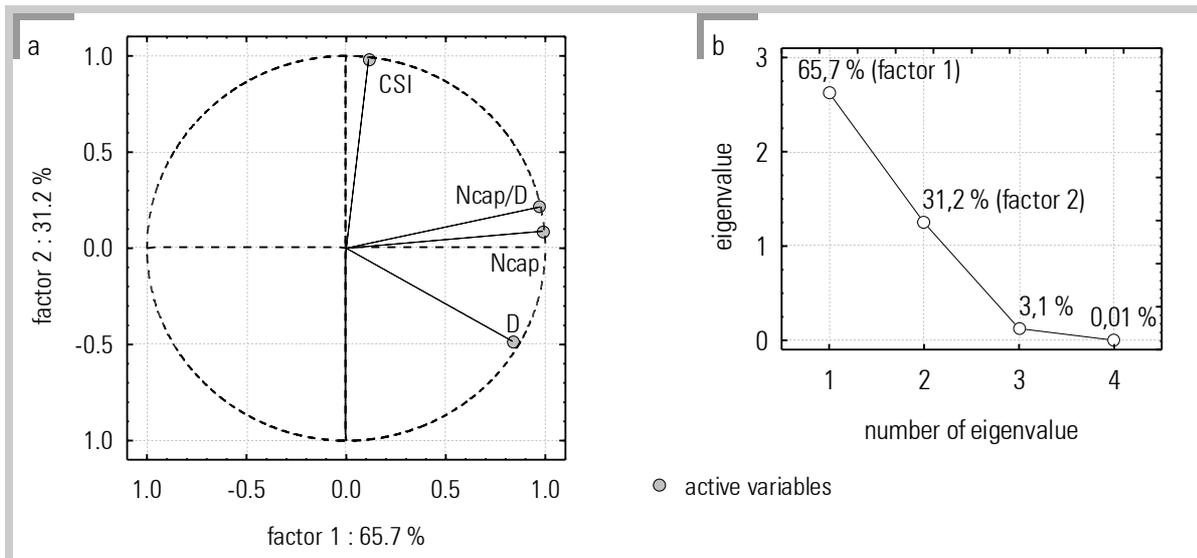


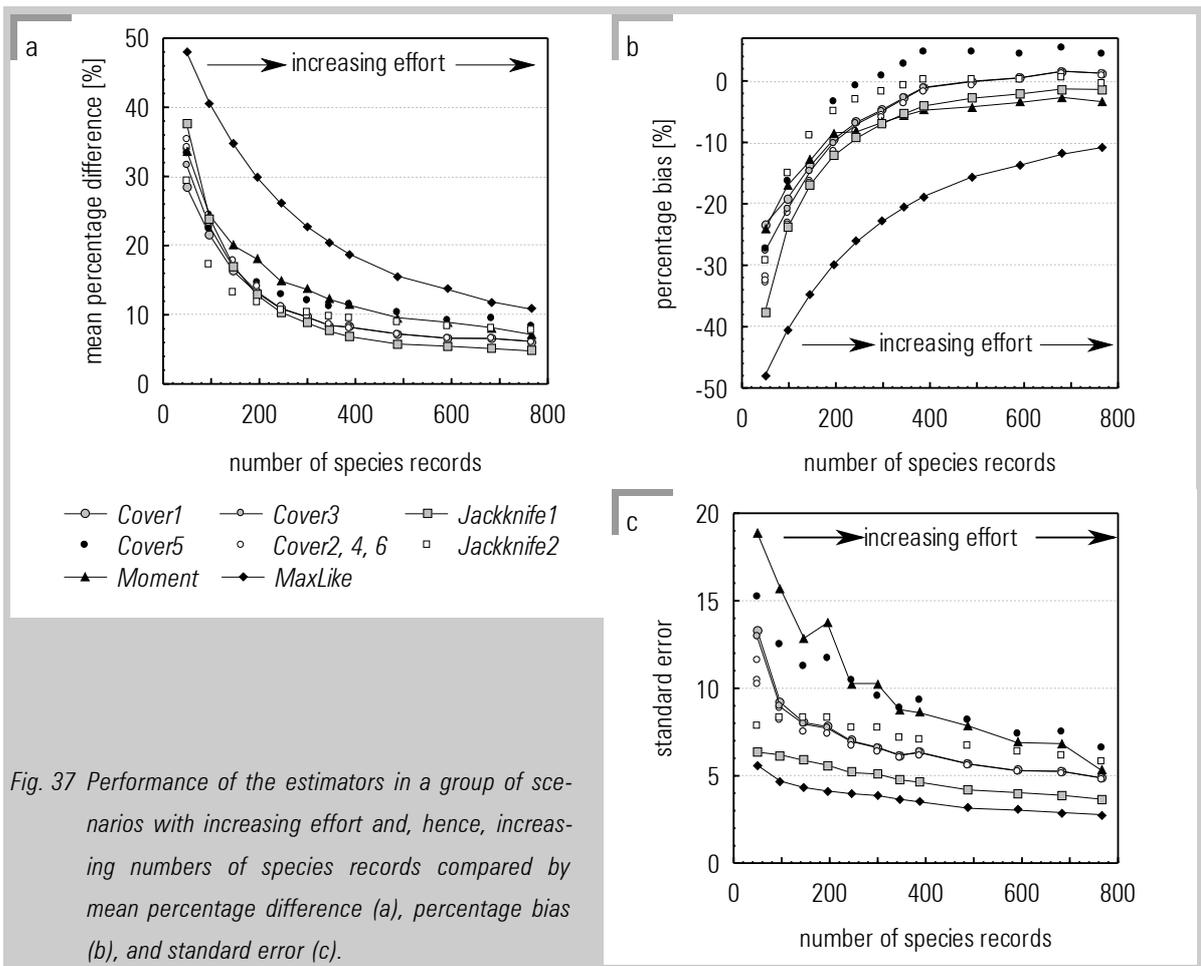
Fig. 36 PCA plot showing the orientation of the parameters in relation to the first two axes (a) and the contribution of the factors to the total variance (b).

was oriented parallel to the axis of the second factor (Fig. 36a). The two strongest factors of the PCA explained nearly all of the total variance (96,9%) and had high eigenvalues (Fig. 36b). The number of recorded species (D) had an intermediate position between the two main factors of the PCA (Fig. 36a). The quotient of the number of species records and recorded species (Ncap/D) was always highly correlated to the number of recorded species (Fig. 36a). Since the number of species records (Ncap) and the CSI were the two parameters most closely related to the first two axes of the PCA, these were selected for further study as to whether they could be used as criteria to predict the performance of species richness estimators.

5.3.2 Performance of the estimators

In order to show the role of the number of species records on the accuracy of the species richness estimators a group of scenarios had to be found, in which the number of species records changes, however, the CSI stays constant. This condition is met by scenarios with increasing effort implemented by an increasing number of periods. In this group of scenarios the number of species records increased, whereas, the CSI changed only a little because an increasing number of sampling periods covered an increasing part of the temporal variability. Thus, the effect on the accuracy of the species richness estimates can be supposed to originate from the changes in the number of species records in these scenarios.

Generally, increasing the effort in these scenarios resulted in an increasing number of species records which was again correlated with an increasing accuracy of the estimates (Fig. 37). The mean percentage difference between the "true" species number and the estimated species number, the per-



percentage bias, as well as the standard error clearly decreased with an increasing number of species records. All estimators underestimated the “true” species richness when the effort was low and, hence, the number of species records was small.

The coverage estimators (*CoverX*) except for *Cover5* performed similarly in terms of the mean percentage difference (Fig. 37a), the percentage bias (Fig. 37b), and the standard error (Fig. 37c). *Cover5* is the only estimator which clearly overestimated the “true” species richness in case of high numbers of species records. Moreover it showed a higher standard error than the other coverage estimators and a higher mean percentage difference. Except in the case of very low numbers of species records, *Jackknife1* reached the smallest mean percentage difference and a small standard error (Fig. 37c). However, if the numbers of records were small, it had a stronger tendency to underestimate the “true” species numbers than other estimators (Fig. 37b) except *MaxLike*. If the numbers of species records were high, *Jackknife2* showed quite a high standard error and an increased mean percentage difference. On the other hand it was only a little biased by comparison.

In these scenarios, the moment estimator (*Moment*) showed a similarly good performance like the other estimators (Fig. 37a,b). However, the standard error was mostly comparably high (Fig. 37c).

Thus, it seems to be less reliable than most of the other estimators. The mean percentage difference of *MaxLike* was the highest of all estimators and it underestimated the most (Fig. 37). However, the standard error was rather small. This confirms that a small standard error does not indicate the accuracy and reliability of an estimator, if the assumptions of the estimator are violated. The use of *MaxLike* would assume equal recording probabilities of the members of a species community. As these scenarios confirmed that it is unreasonable to estimate species richness with an estimator assuming equal recording probabilities of the species, this estimator is omitted in the following.

The curve shape index (CSI) is the other parameter whose effect on the performance of the estimators is studied (see Chapter 5.3.1). The CSI did not change in any of the simulated scenarios, without a simultaneous change in the number of species records. Nevertheless, in the case of the selected group of scenarios with their increasing heterogeneity of samples caused by a combination of all simulated sources of it, the CSI and the number of species records did not change simultaneously. Although increasing heterogeneity first decreased the CSI and later increased it again, the number of species records steadily grew (Fig. 38c). Hence, these scenarios are appropriate to study the effect of the CSI on the performance of the species richness estimators.

Increasing heterogeneity in this group of scenarios caused a decreasing CSI on the right half of the curve. This means that a larger proportion of the recorded species became rare and probably that the recording probability of each single species decreased, although the number of recordings increased. In the scenarios above (Fig. 37), an increasing number of species records improved the quality of the estimation of species richness in all estimators. In these scenarios, the rapidly decreasing CSI (right part of the plots) hinders this (Fig. 38b,c). Thus, the mean percentage difference and the percentage bias increased as long as the CSI decreased rapidly. However, on the left side of the curve the complex combination of heterogeneities of this simulation caused the CSI to increase again and, hence, drastically improved the quality of the estimates together with the steadily increasing number of species records (Fig. 38a). In contrast, the standard error of the estimates was little affected.

In these scenarios, *Cover1* and *Cover3* performed best among the coverage estimators in terms of mean percentage difference and percentage bias (Fig. 38). The other coverage estimators showed more or less pronounced mean percentage differences and underestimation, which suggests that these estimators are not very robust against this kind of heterogeneity. The estimates from *Jackknife1* were the most accurate estimates with the exception of the percentage bias in the middle of the curve. The performance of *Jackknife2* was quite constant in terms of the mean percentage difference. Thus, it performed better or worse than the other estimators depending on the combination of CSI and the number of species records. Although the percentage bias was small, *Jackknife2* offered little reliability because of the high standard error of the simulated estimation results. In terms of percentage bias, *Moment* was comparable to the best performing estimators like *Jackknife1*. However, its mean percent-

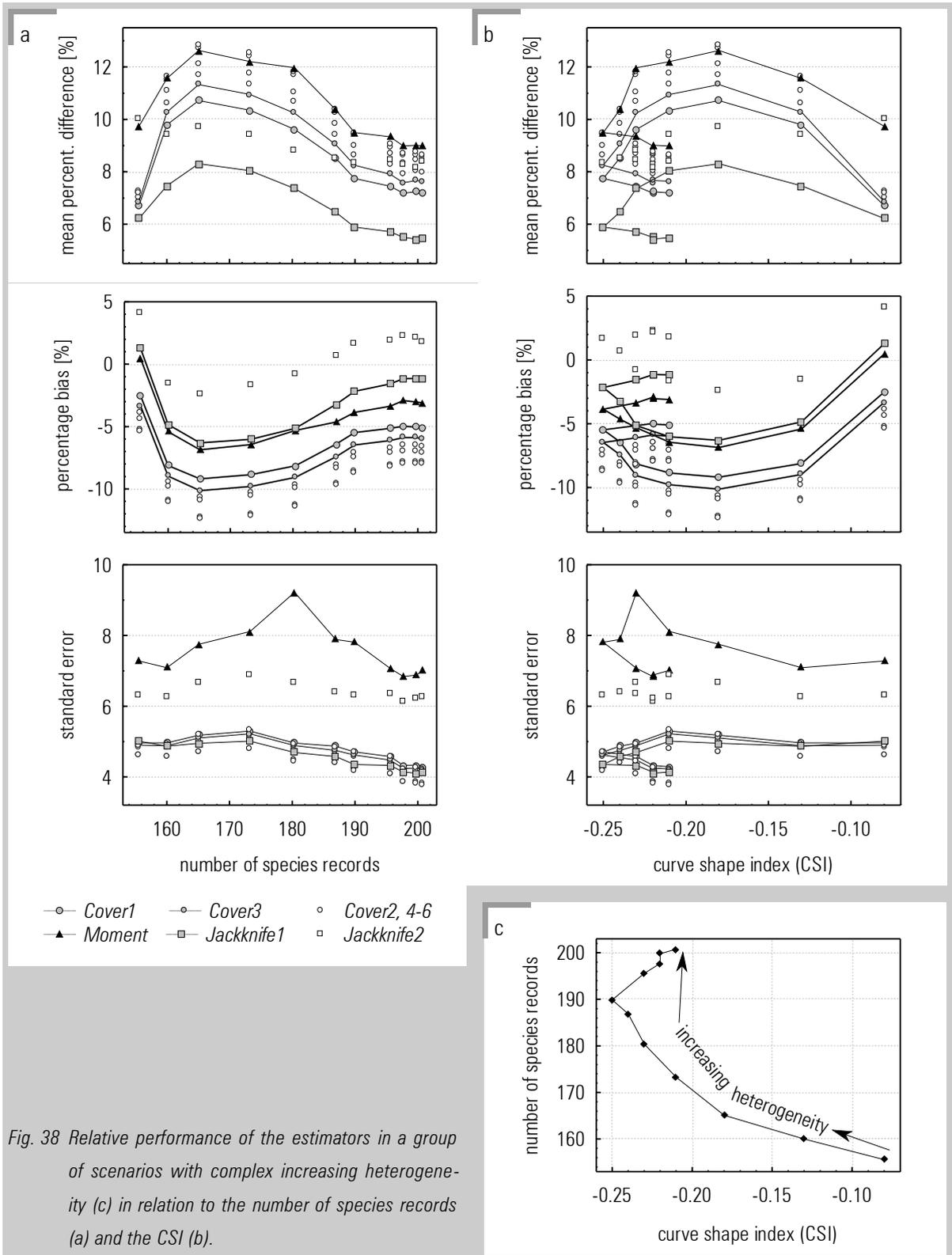


Fig. 38 Relative performance of the estimators in a group of scenarios with complex increasing heterogeneity (c) in relation to the number of species records (a) and the CSI (b).

age difference was high and it always had the highest standard error of all estimators (Fig. 38). Thus, its results are highly unreliable.

The following two groups of scenarios were chosen to show that changing one factor can increase the number of species records and increase the CSI, whereas changing other factors can increase the number of species records, however, decrease the CSI (Fig. 39c). The plot with increasing numbers of species records and increasing CSI originates from a simulation with an increasing mean range on the habitat axis, along which virtual species can be recorded. This means that the species' recording probability increased in a steady habitat and with the same trapping method. The other plot originates from a simulation, in which the effort was constant but the ratio of sites and periods shifted from a few sites over lots of periods to a lot of sites over a few periods. This shifts the heterogeneity from a temporally-dominated to a spatially-dominated one. Thus, in the temporal samples of this group of scenarios, the decreasing temporal heterogeneity increased the CSI, but did not prevent the number of species records from decreasing.

The light gray symbols mark the trivial case of increasing trapping success and consequently increasing the recording probability of the species. This caused both increasing numbers of species records and an increasing CSI both improving the quality of the estimates (Fig. 39a,b). These scenarios are typical for changing recording probabilities of the species with constant spatial or temporal heterogeneity. In these cases the numbers of species records increased as well as the values of the CSI (Fig. 39c). The dark gray marks the case of the number of species records and the CSI balancing each others effect in terms of accuracy and reliability of the species number estimates (Fig. 39a,b). This appeared in scenarios, when the positive effect of decreasing heterogeneity and consequently increasing values of the CSI (Fig. 39c) on the accuracy of the estimates was not strong enough to counterbalance the negative effect from decreasing numbers of species records.

Again, *Cover1* was the most successful among the coverage estimators. As for the scenarios described above *Jackknife1* was usually a bit more accurate (Fig. 39a,b). However, *Cover1* showed the smaller mean percentage difference and the smaller percentage bias, when the CSI was high and the number of species records low. *Moment* again showed a small percentage bias but mostly the highest mean percentage difference and standard error.

In groups of scenarios used to analyze the sampling design, a constant number of traps was grouped to different numbers of sites. Thus, in this group of scenarios the effort stayed constant whereas the number of samples changed (Fig. 40a). As the number of samples (t) is an important parameter in species richness estimators, it can be hypothesized that such a change in the sampling design may result in a changing relative performance of the estimators. A large number of sites, which are the samples in this case, with a small number of traps covers more heterogeneity than a small number of sites with a large number of traps. Therefore, the number of species records increased

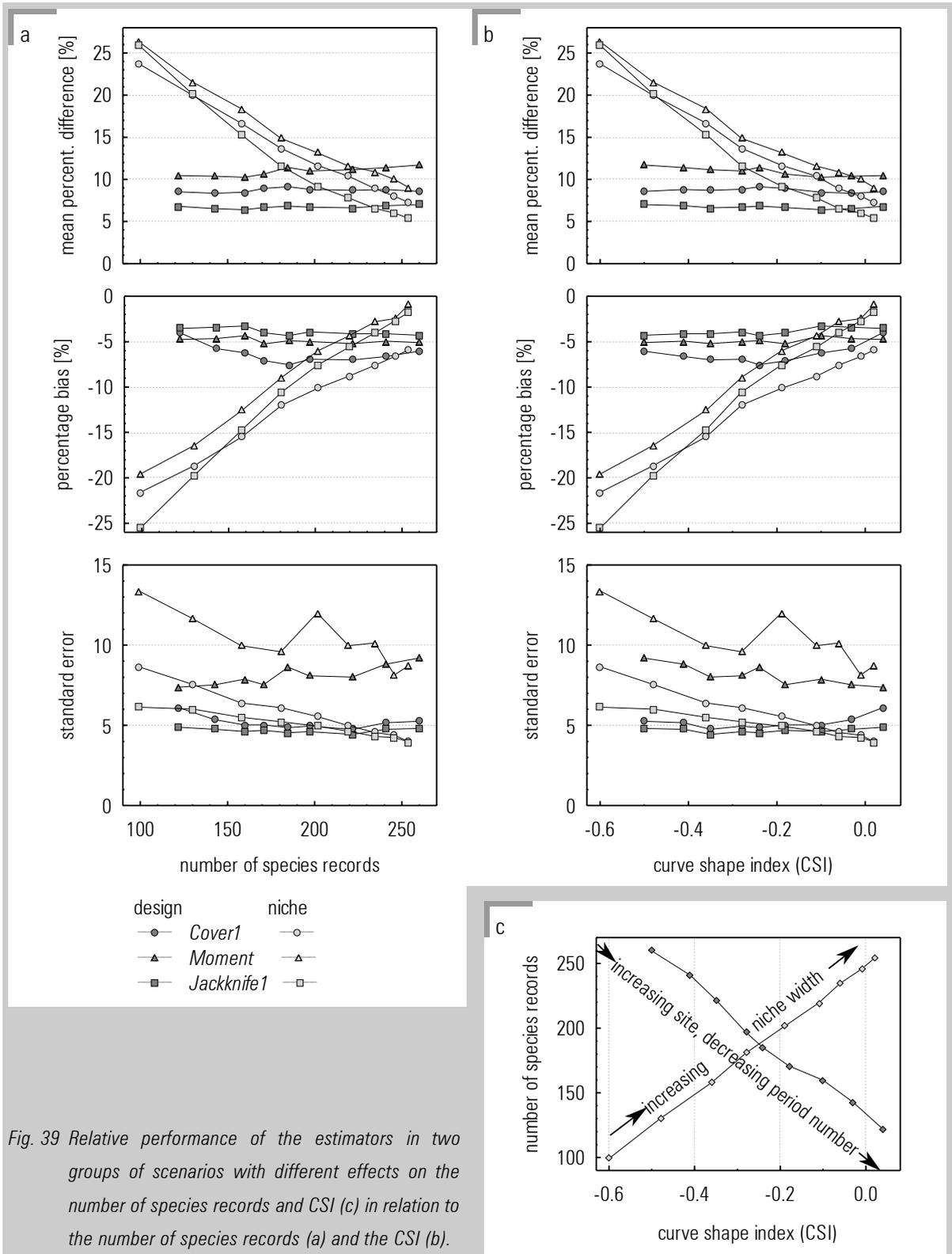
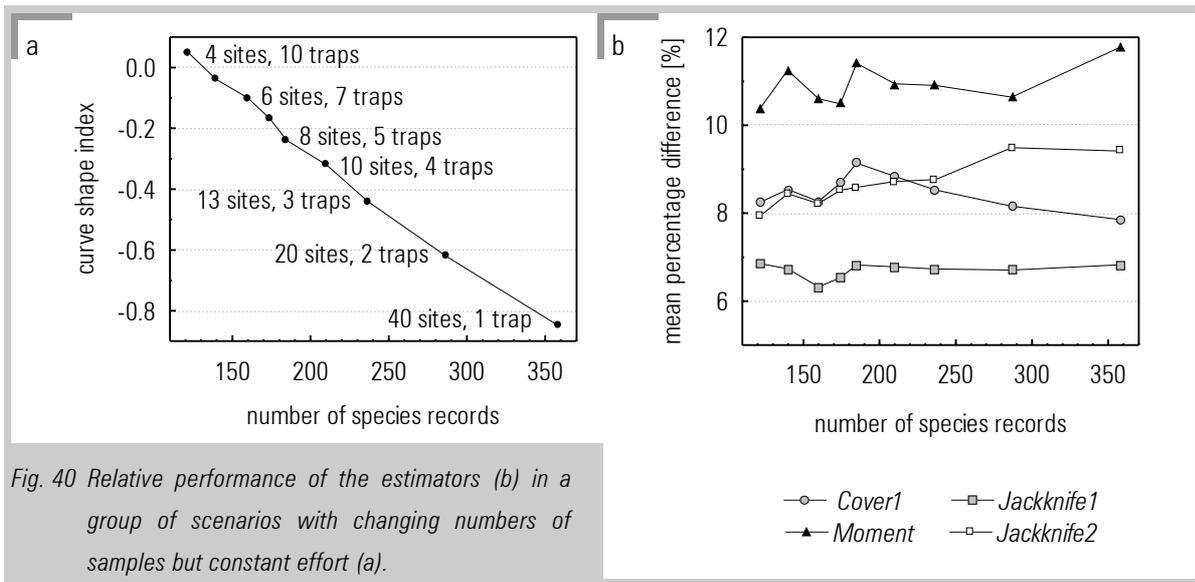


Fig. 39 Relative performance of the estimators in two groups of scenarios with different effects on the number of species records and CSI (c) in relation to the number of species records (a) and the CSI (b).



whereas the CSI decreased according to this change (Fig. 40a).

Neither the performance of the estimators changed substantially in response to changing the design nor were the estimators clearly different in their reaction (Fig. 40b). The effects of the increasing number of species records and the decreasing CSI balanced each other out. Thus, these scenarios did not give a clear indication as to which design to use, whether a few sites with many traps or many sites with (in the extreme case) single traps.

5.3.3 Detailed comparison of the most promising estimators

It was shown above that the number of species records and the CSI are related to the accuracy of the species richness estimates of the studied estimators. In order to assess the strong points and shortcomings of the estimators, the three most promising are compared in terms of mean percentage difference, percentage bias, and standard error as a function of the number of species records and the CSI. These measures of accuracy of the species richness estimates are shown as contours of equal values in a grid of numbers of species records and CSI for single estimators (Fig. 41). The contour plots are based on all scenarios dealing with different sources of heterogeneity and effort. The data points in Figure 41 show the ranges over which the simula-

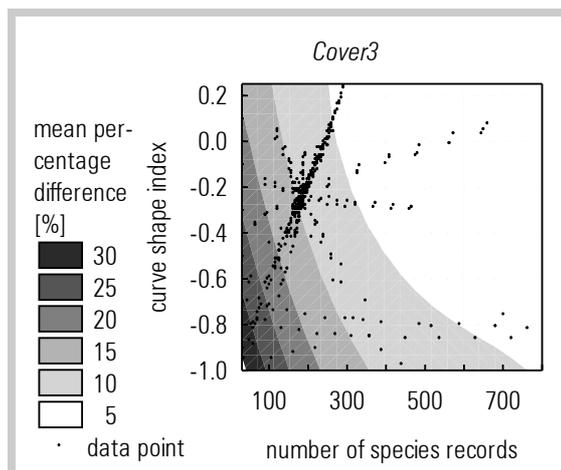


Fig. 41 Performance of Cover3 in terms of the mean percentage difference of the estimates as a function of the number of species records and the CSI. The contour plots are interpolated on the basis of the data points shown.

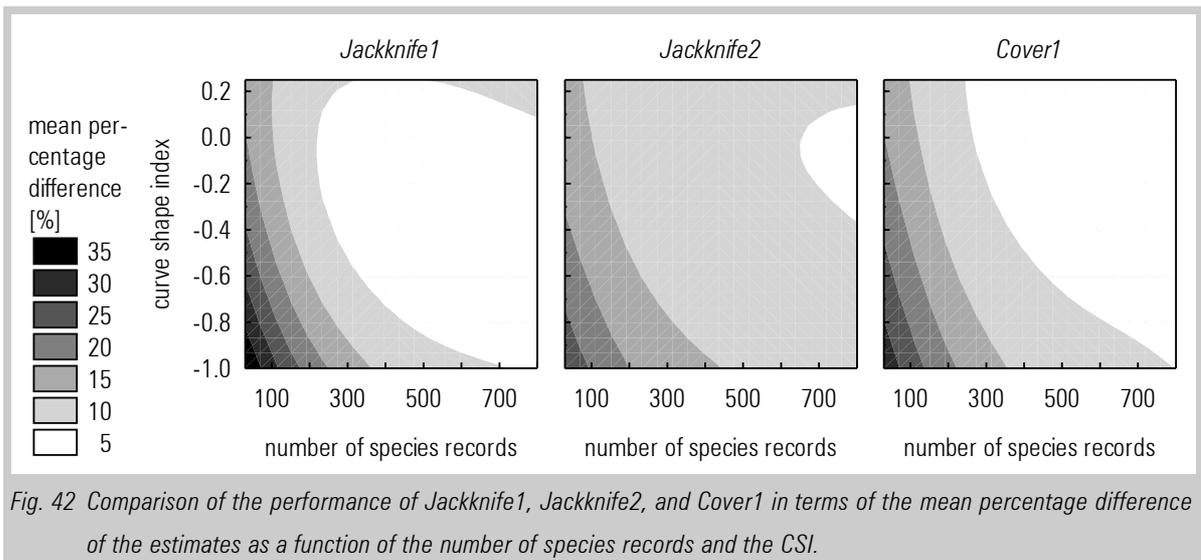


Fig. 42 Comparison of the performance of *Jackknife1*, *Jackknife2*, and *Cover1* in terms of the mean percentage difference of the estimates as a function of the number of species records and the CSI.

tion provided values of the number of species records and the CSI and which ranges were interpolated.

First the estimators were compared in terms of the mean percentage difference of the simulated estimates as a function of the number of species records and the CSI. *Jackknife1* showed the largest area of small mean percentage differences to the “true” number of species, closely followed by *Cover1* (Fig. 42). However, the performance of *Jackknife1* was weaker than that of *Cover1*, if the number of species records was high and the CSI was very low. *Jackknife2* did not achieve the same accuracy as both of the other estimators. *Cover3* always performed very similarly to *Cover1* but a bit worse (Fig. 41, Fig. 42), thus, it is omitted in the following.

In terms of percentage bias, both jackknife estimators were similar (Fig. 43). The values of the mean percentage bias of *Cover1* were low for a wide range of the number of species records and the CSI. However, for the larger part of the parameter space, they were slightly higher than that of the jack-

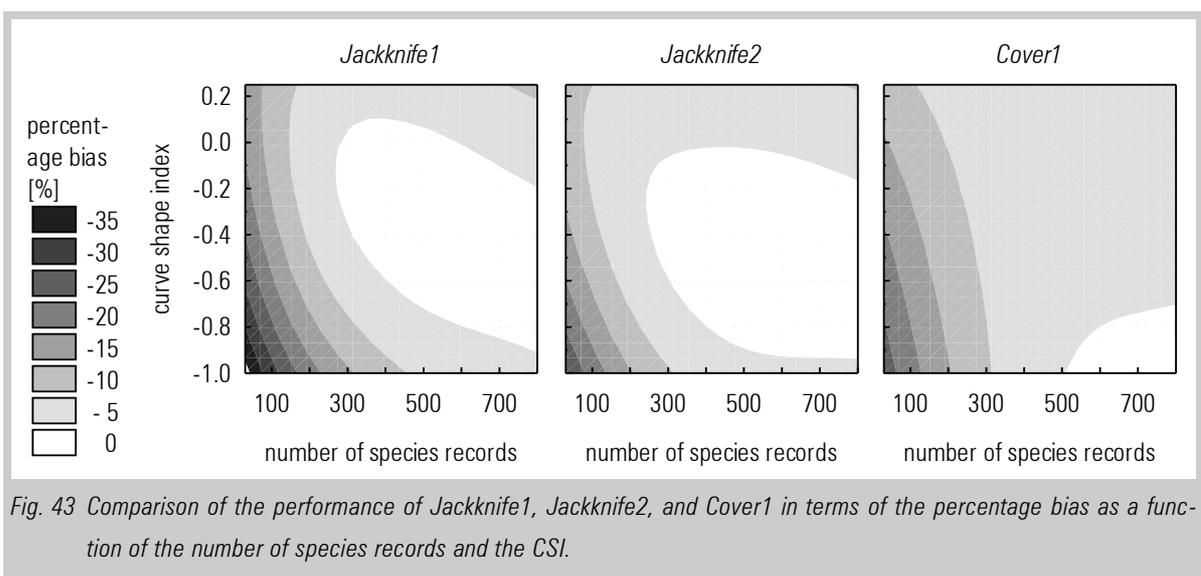


Fig. 43 Comparison of the performance of *Jackknife1*, *Jackknife2*, and *Cover1* in terms of the percentage bias as a function of the number of species records and the CSI.

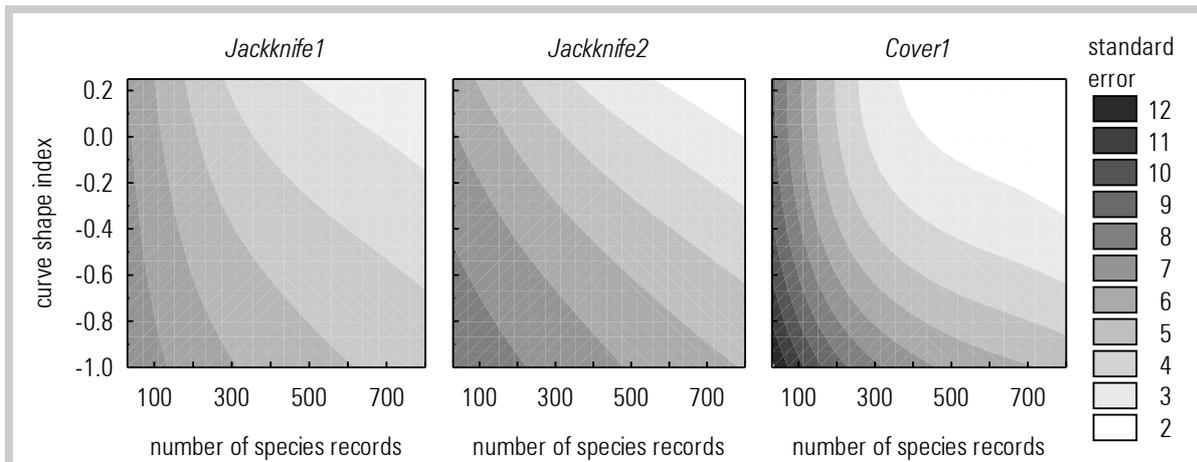


Fig. 44 Comparison of the performance of *Jackknife1*, *Jackknife2*, and *Cover1* in terms of the standard error as a function of the number of species records and the CSI.

knife estimators. For very high values of the CSI all three estimators performed equally well. *Cover1* performed better than the other estimators in the case of high numbers of species records together with high values of the CSI.

In terms of the standard error of the simulated estimates, *Jackknife1* performed well in that area of the parameter space where it did not perform at its best in the two comparisons above (Fig. 44). *Jackknife2* usually performed worse than the other two. *Cover1* was the most reliable estimator, if the number of species records was high and the CSI was high, which is usually the case for high sampling effort. In the area with low values for the CSI and small numbers of species records *Cover1* displayed high values for the standard error. Thus, in such cases *Cover1* is probably more accurate than *Jackknife1* but less reliable.

5.3.4 Ranking the estimators by their performance

The first group of scenarios, which was selected to compare the estimators in a further step of integration by ranking, was used above to show the effects of the CSI on the performance of the estimators (Fig. 38a,b). In this group of scenarios, the heterogeneity as a combination of all simulated sources of it increased. The ranking again reflected the change in the relative performance of the estimators in the case of small numbers of species records (Fig. 45). The ranks in terms of mean percentage difference showed a complex pattern but clear advantages of the *Jackknife1*, *Cover1*, and *Cover3* (Fig. 45a). As shown above, *Jackknife1*, *Jackknife2*, and *Moment* had a low bias and ranked well in this case (Fig. 45b). *Cover6* showed that an estimator with bad ranks in the mean percentage difference and the percentage bias nevertheless can be ranked well in the standard error (Fig. 45c).

In terms of the weighted mean ranks, estimators which performed best were those which were balanced best in all three measures of quality. These are clearly *Jackknife1*, *Cover1*, *Cover3*, and partly

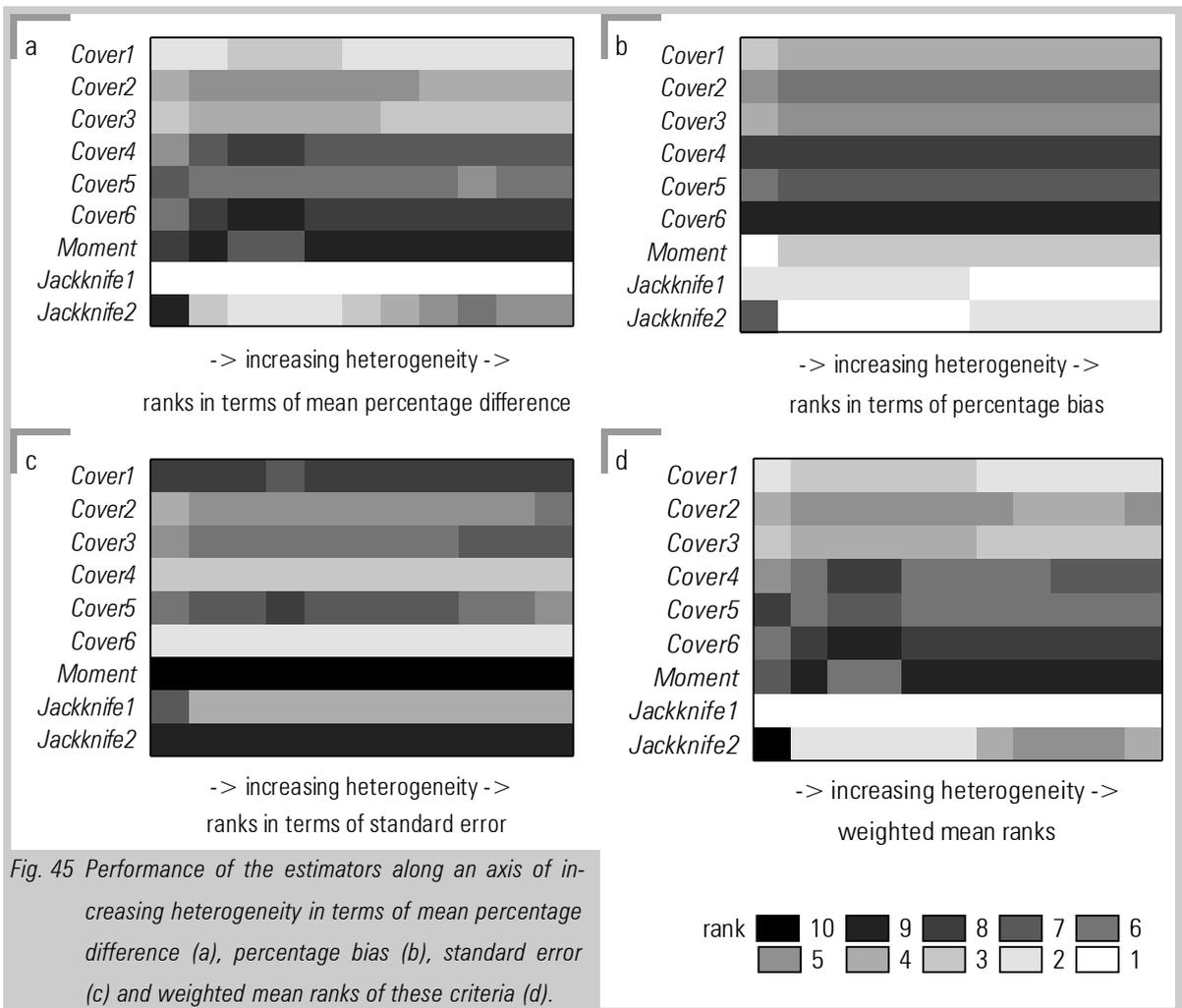
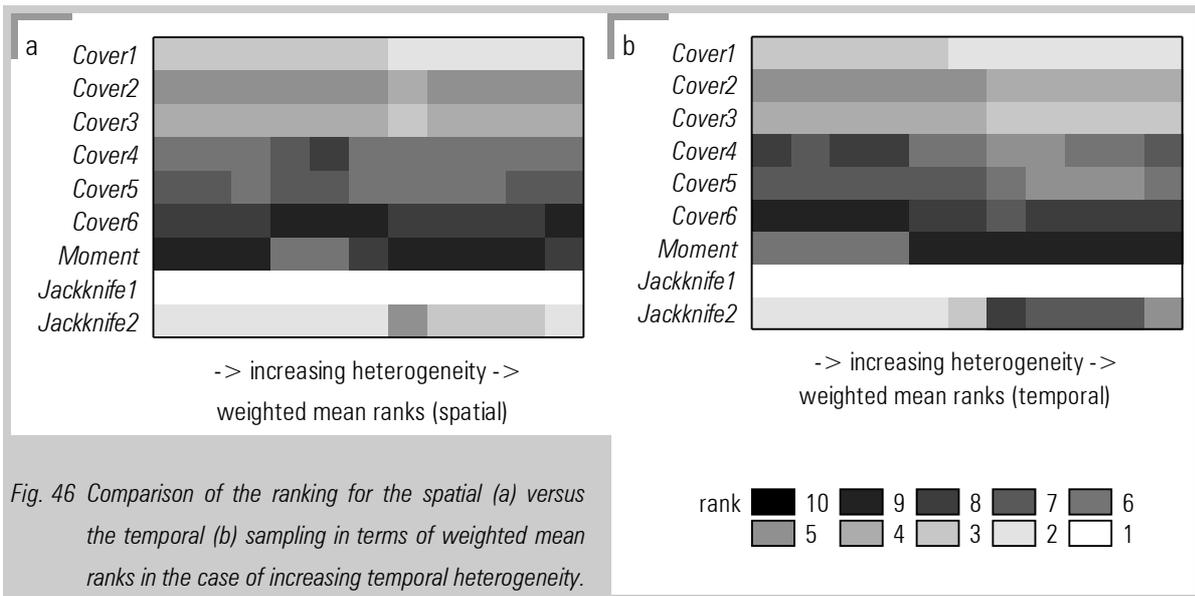


Fig. 45 Performance of the estimators along an axis of increasing heterogeneity in terms of mean percentage difference (a), percentage bias (b), standard error (c) and weighted mean ranks of these criteria (d).

Jackknife2 (Fig. 45d). A small standard error in particular is not sufficient criteria for an accurate and reliable estimator (Fig. 45c,d). The patterns of ranks (Fig. 45) showed the ability of the estimators to cope with different combinations of values of CSI and number of species records, which were caused by complex sources of increasing heterogeneity (Fig. 38).

In the following scenarios, the strength of the spatial heterogeneity differed strongly from the temporal one. The pattern of the estimators' ranks differed depending on the use of the simulated data. *Jackknife2*, for example, continued to be a good estimator with increasing heterogeneity when the simulated records were used spatially (Fig. 46a), whereas it was ranked worse with higher heterogeneity in the temporal case (Fig. 46b). On the other hand, *Cover1* and *Cover3* performed better in the temporal case when heterogeneity was high. These differences appear for example, when a strong heterogeneity of the periods affects the CSI and the number of species records more if using the periods as samples instead of the sites as samples. Nevertheless, *Jackknife1* remained the most useful estimator and most of the changes occurred for the worse estimators (Fig. 46).



Finally a group of scenarios was selected to compare the performance of the estimators in the case of increasing effort resulting in increasing numbers of species records and increasing CSI. For minimum

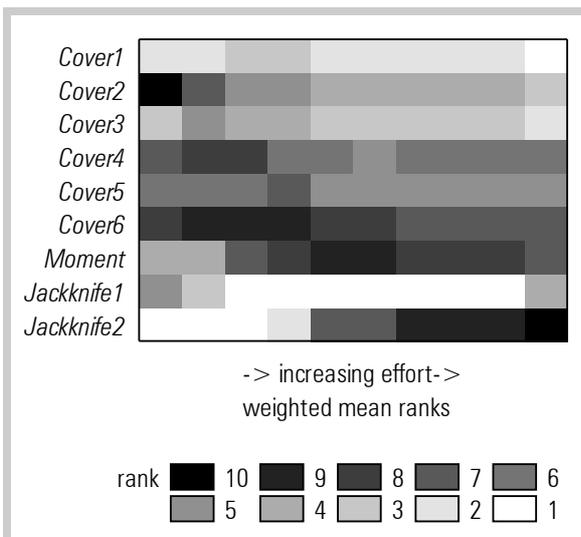


Fig. 47 Comparison of the estimators performance in terms of weighted mean ranks in a group of scenarios with increasing effort.

effort, *Jackknife2* achieved the best ranks, for intermediate effort *Jackknife1*, *Cover1*, and *Cover3* were best, whereas for maximum effort *Jackknife1* seemed to get even worse (Fig. 47). On the one hand, this shows that increasing effort changed the relative performance of the estimators. On the other hand, this hides the fact that all the methods of estimating species richness reached a higher accuracy and reliability and the differences between them decreased, when the number of species records and the CSI increased.

Tab. 5 Global ranks of the estimators in the simulation.

<i>Jackknife1</i>	1
<i>Cover1</i>	2
<i>Cover3</i>	3
<i>Jackknife2</i>	4
<i>Cover2</i>	5
<i>Cover5</i>	6
<i>Cover4</i>	7
<i>Moment</i>	8
<i>Cover6</i>	9
(<i>MaxLike</i>)	10)

Across all scenarios of the simulation *Jackknife1* was marginally the most accurate and reliable estimator for species richness in terms of weighted mean ranks (Tab. 5). *Cover1* and *Cover3* were similarly accurate. *Jackknife2* lacked reliability in many situations. The rest of the estimators did not reach the accuracy and reliability of these four and, consequently,

achieved worse ranks (Tab. 5).

The results of the ranking can be condensed in order to identify the areas where the four best estimators performed relatively well in terms of the number of species records and the CSI (Fig. 48). The number of species records referred to the standard "true" number of species of 60. The plot was based on all simulations dealing with different sources of heterogeneity and

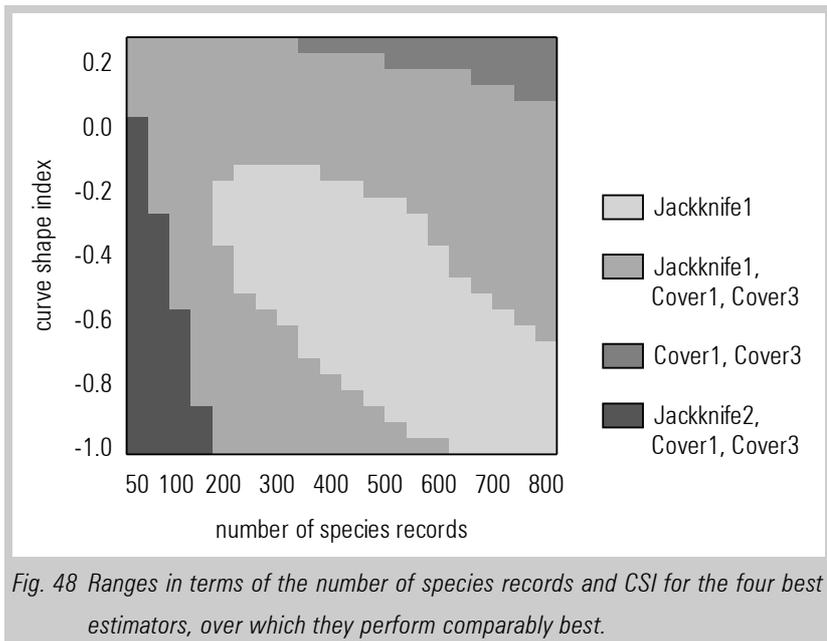


Fig. 48 Ranges in terms of the number of species records and CSI for the four best estimators, over which they perform comparably best.

with effort. It shows the performance of these four estimators concluded from the mean weighted ranks as well as the ranks in terms of mean percentage difference to the "true" species number, percentage bias and standard error. This led to guidelines as to when to use which species richness estimator in terms of the number of species records and the CSI viewed in the form of areas (Fig. 48). This figure demonstrates the following rules of thumb to select the most appropriate estimator:

1. *Jackknife1* is usually the most accurate and reliable estimator, however, over a broad range of parameter space it can be replaced by *Cover1* or *Cover3*.
2. *Cover1* is slightly less accurate and reliable, however, it performed well in the case of
 - low CSI (< -0.8) combined with low numbers of species records (< 300)
 - high CSI (> 0.0) combined with higher numbers of species records (> 300).
3. *Cover3* is nearly as accurate and reliable as *Cover1* and can be used instead of *Cover1*.
4. *Jackknife2* is less accurate and reliable, however, it can be used in the case of a very low number of species records (< 150) and relatively low CSI (< -0.1).

5.4 Discussion

5.4.1 Simulation

It is usually impossible to know the “true” number of species in field inventories. In order to avoid such uncertainty when studying the performance of methods of estimating species richness, simulations are required. The estimation of species richness using mark-recapture statistics is based on the recording frequencies of the species, at least on f_1 (BURNHAM & OVERTON 1978), on f_1 and f_2 (BURNHAM & OVERTON 1978, CHAO 1984), or on more of the recording frequencies (CHAO ET AL. 1992), as well as on the number (of incidences) of species records.

Although a huge amount of work was done on species richness estimation, only a few published distributions of species' recording frequencies are available (CODDINGTON ET AL. 1996). Even in papers using nonparametric estimators for species richness estimation, the recording frequencies of the species of the studied community were not shown. Simulations, which were done in order to study the estimators of species richness, were always based on the fixed distributions of recording probabilities. In order to model these recording probability distributions, BURNHAM & OVERTON (1979) used constant values, CHAO (1987) attributed fixed recording probabilities to different sections of the simulated species community and both used the uniform and the beta distribution.

This method of creating the distribution of species' recording frequencies, expressed as CSI, and the numbers of species records has a marked disadvantage, namely that factors affecting the CSI and the numbers of species records are fixed. Hence, these factors such as effort, effects of species characteristics like habitat use, spatial and temporal heterogeneity of the samples, and characteristics of the species community like dominance structure (see Chapter 3.4.2) cannot be varied in the simulation. Thus, this concept of simulation cannot be used when trying to distinguish the influences of these factors on the distribution of species' recording frequencies, the numbers of species records, and, hence, on the accuracy and reliability of the estimates of different estimators.

Thus, for the purpose of this study, comparing the performance of species richness estimators in relation to such factors, a different concept of simulating the species' recording frequencies and the number of species records was required. First, a basic distribution of species' recording probabilities had to be defined. Field data clearly indicate that most species are more or less rarely recorded and only a few of them regularly. This can be approximated by the beta distribution used by BURNHAM & OVERTON (1979) and CHAO (1987) as well as by the density function of the exponential distribution used in this study. The simulated differences of sampling sites and periods as well as the differences of the species characteristics expressed as their behavior in a simple habitat model, modified these recording probabilities. In this way factors like sampling effort, the differences in sites and periods, and differences in the characteristics of species groups were reflected in the simulation. Comparing the distribu-

tions of species' recording frequencies from the simulation with those from the field showed, that the simulation reflected the situation in the field (see Chapters 3 and 4).

Because of the effort, it was necessary to perform most of the simulations with one basic number of 60 "true" species. This number of species fits quite well with the numbers in the field found in carabid beetles, epigeal spiders, and plants and is higher than those of the molluscs (DEICHNER ET AL. 2003). However, the number of butterfly species in tropical regions for example can be much higher (SOBERÓN & LLORENTE 1993), in which case the number of species records would also be higher. Hence the range of the simulation does not cover the whole range of possible numbers of species records.

5.4.2 *Factors affecting the accuracy of species richness estimation*

The selected simulation scenarios in terms of differences in effort, heterogeneity in the samples, and characteristics of the species groups (niche width) showed the effect of these factors on the accuracy and the reliability of the estimates of all studied species richness estimators. Moreover, the relative performance of the estimators was also affected by the result of a complex interaction of these factors. Thus, attempting to use field data to derive simple rules which make it possible to select the most accurate and reliable estimator based on these factors turned out to be very difficult. Even if it was possible to derive values for most of these factors from field data, this would not make it possible to select the best species richness estimator. The rules to select the most appropriate estimator would be too complicated to be useful.

On the other hand, independently from the factors that changed the number of species records and the curve shape index (CSI), the accuracy and reliability of the estimates consistently correlated with these parameters. These two parameters integrated all these factors and directly affected the accuracy and reliability of the species richness estimates. Therefore, the number of recorded species and the CSI of the distribution of species' recording frequencies were chosen to indicate the appropriate estimator.

BURNHAM & OVERTON (1979) stated that any "design with t identified units of equal effort" are useful samples for species richness estimation. This statement was made in the context of applying the jack-knife method, developed to estimate population size, on the estimation of species richness. As data sets for estimating population size are mostly temporal and data sets for estimating species richness are mostly spatial, this implies that BURNHAM & OVERTON (1979) do not recognize a basic difference between spatial and temporal samples. However, comparing the spatial and temporal use of the simulated species records showed that the CSI can be very different caused by differences between the extent of spatial and temporal heterogeneity respectively in the samples (see Chapter 4.3.3). As the CSI was shown to affect the performance of species richness estimators this aspect of sampling design for species richness estimation needs some discussion, particularly because this is not explicitly

discussed in the literature on species richness estimation and heterogeneity is demonstrated as a problem to be avoided.

When sampling plants on sites over consecutive periods, the species lists will be nearly identical, if they are summed up for the periods, but different, if they are summed up for the sites. When estimating the species number with such temporal samples, the number of counted species will nearly reach the number of estimated species because of the small temporal heterogeneity. This is not a mistake, as it is unlikely to see many new species when increasing the effort by adding the data from further sampling periods. When estimating species richness based on such spatial samples, the estimates will be much higher although the number of recorded species stays the same. This is also correct because the heterogeneity of sites makes it probable that an additional site contains new species. This means that depending on the sampling design, the species records and estimates of species richness reflect the variability of the sampled species community in different ways. Hence, no estimator is able to estimate the unseen species of the sites by using a temporal sampling design and vice versa, when temporal heterogeneity differs strongly from that of the spatial. Therefore, it can not generally be advised to avoid heterogeneity in samples.

5.4.3 Performance of the estimators

The estimators studied above were originally developed to estimate population size in the case of heterogeneity in the capture probability of individuals. Thus, simulations used to compare these estimators were applied against the background of the conditions for estimating population size (BURNHAM & OVERTON 1978, CHAO ET AL. 1992). In order to compare the estimators in their usefulness for species richness estimation, selected sets of field data were used to compare the estimated results with educated guesses about the “true” number of species (PALMER 1990, COLWELL & CODDINGTON 1994). Only WALTHER & MORAND 1998 used their parasite data to additionally compare some estimators by simulation. Consequently, at present these methods of estimating species richness are hardly evaluated by simulations, which concentrate on species numbers.

Among the nonparametric estimators of species richness, the jackknife concept is the most frequently used. *Jackknife1* was the most accurate and reliable estimator for species richness estimation in this study. This confirms earlier studies in which *Jackknife1* was also shown to perform well (PALMER 1990, PALMER 1991, COLWELL & CODDINGTON 1994, CHAZDON ET AL. 1998, WALTHER & MORAND 1998, BROSE & MARTINEZ 2004). It tends to underestimate, however, in a relatively small range. *Jackknife2* was also evaluated well (PALMER 1991), however, this simulation showed that it clearly overestimates when the number of species records gets larger and it lacks reliability in many situations.

Similar to the performance of *Jackknife1* was the performance of *Cover1* and *Cover3*. Their estimation of the coefficient of variation ($\hat{\gamma}^2$) includes a term, which reflects the differences of the general

recording probabilities of sites or periods (model M_{th}). This might be responsible for the advantage of these two estimators. In *Cover2* the estimation of the coverage \hat{C} seems to be less suitable for estimating species numbers. For the rest of the coverage estimators studied in the simulation, which all use the same estimator of \hat{C} as in *Cover1*, the estimation of the coefficient of variation seems to be less successful. Even if *Cover1* and *Cover3* tend to underestimate the “true” species richness slightly, they provide accurate and reliable estimates.

The rest of the coverage estimators showed a higher mean percentage difference. The concept of coverage has been used several times to estimate species richness (e.g. COLWELL & CODDINGTON 1994, CHAZDON ET AL. 1998). However, there is only one incidence-based coverage estimator (ICE) which has been studied several times until now (on the basis of field data). The reports about its quality are contradictory. With bird data (CHAZDON ET AL. 1998) and a simulation with variable mobility of the species (BROSE & MARTINEZ 2004) it performed well, with parasite data (WALTHER & MORAND 1998) and a simulation with variable effort and spatial patterns (BROSE ET AL. 2003) it did not. In this study the ICE (LEE & CHAO 1994, CHAZDON ET AL. 1998) has not been tested. The most similar estimator in this study is *Cover6* (CHAO & LEE 1993), which is slightly different in the estimation of the coefficient of variation ($\hat{\gamma}^2$). It did not perform well, because it tended to underestimate like the worse group of coverage estimators (*Cover2*, 4) and additionally showed a slightly higher standard error. *Cover5* is the only estimator which frequently overestimates the “true” species richness. Compared to *Jackknife1*, *Cover1*, and *Cover3* these coverage estimators showed a clearly worse performance. The abundance-based estimators (ACE) are reported not to work well (COLWELL & CODDINGTON 1994, CHAZDON ET AL. 1998) and were not studied here.

In this study *Moment* displayed a small percentage bias, however it had numerous outliers, which caused a high mean percentage difference from the “true” number of species and a high standard error. This means that although *Moment* can offer accurate results, these are hardly reliable. WALTHER & MORAND (1998) reported that the incidence-based moment estimator worked well for their data on parasites. The simulation of WALTHER & MORAND (1998) also showed the small bias of this estimator, however, the reliability of the estimates was not studied.

Although its standard error was usually very small, *MaxLike* can not be used for species number estimation as it severely underestimated the “true” species richness. The maximum likelihood estimator used in this study has been developed to estimate abundances under the assumption of equal capture probability. Thus, it had to be expected that *MaxLike* fails to accurately estimate species richness, because the probabilities of species to be recorded are always heterogeneous. However, it is important to observe that the violation of the assumptions of this method really led to a severe underestimation of the “true” species number. On the other hand, *MaxLike* showed a small standard error, calculated from the simulation runs. This confirms that a small standard error is never a criteria for an accurate estimate, if the assumptions of the method are violated.

The formulas for the estimated square of the coefficient of variation \hat{y}^2 of *Cover1*, *Cover2*, and *Cover3* contain a term representing the heterogeneity of the samples $2 \sum_{i < j} \sum_{j=1}^t n_i n_j$. This term is the main difference between the estimators of the coefficient of variation of these three coverage estimators of species richness and the others studied in the simulation. These three estimators were shown to be the most accurate and reliable coverage estimators of species richness. Thus, this difference in the performance of the coverage estimators seems capable of improving the estimation of the coefficient of variation and, hence, the performance of the coverage estimators of species richness. Consequently, for my part, I agree with BUNGE & FITZPATRICK (1993), who placed their faith in the concept of coverage for nonparametric estimation of species richness.

6 Estimators of standard error compared by simulation

6.1 Introduction

When estimating any value, the associated measures of error also have to be estimated. For each of the species richness estimators used above (see Chapter 5.2.3) methods of estimating variance and, hence, standard error are available (BURNHAM & OVERTON 1978, OTIS ET AL. 1978, CHAO 1984, CHAO ET AL. 1992, CHAO & LEE 1992). However, some of these estimators of variance did not perform well in simulations (OTIS ET AL. 1978, BURNHAM & OVERTON 1979). Moreover, they are not comparable with one another and, thus, introduce an additional source of factors influencing the suitability of the estimators of species number. In order to eliminate this influence, two methods of estimating standard error were chosen, which can be used with all of the species richness estimators.

The bootstrap technique to estimate standard error (EFRON 1981) was already used for the jackknife estimator of species richness (NICHOLS ET AL. 1998B). Chao also suggests using it with some of her estimators (CHAO ET AL. 1996, CHAO ET AL. 2001). A related technique is Tukey's jackknife method (MILLER 1974), which proved its usefulness in estimating standard errors of population parameters (MANLY 1977). In a Monte Carlo study both estimators already proved to be similarly useful in estimating standard errors of point estimates (EFRON 1981). However, there is no comparative study of the performance of the bootstrap and the jackknife method for estimating standard errors with the corresponding methods of the species richness estimators (see Chapter 5.2.3). The aim of this study is to detect the most accurate estimator of standard error for each of the selected estimators of species richness.

6.2 Methods

For each of the species richness estimators (see Chapter 5.2.3) an estimator of standard error is available: the coverage estimators *Cover1* – 6 (CHAO ET AL. 1992, CHAO & LEE 1992), the moment estimator (*Moment*) (CHAO 1984), and the jackknife estimators *Jackknife1* / 2 (BURNHAM & OVERTON 1978) with an additional estimator of standard error proposed by HELTSHE & FORRESTER (1983). In the following, these are called "original estimators" and are shown in detail in the Appendix. The alternative estimators of standard error studied here are Tukey's jackknife method and the bootstrap method (SOKAL & ROHLF 1995).

Bootstrap method:

The concept behind the bootstrap method is to take the simulated species records from the original data, in this case, a large number of random samples with replacement, each of them with n elements. From these random samples the statistic of interest, the species number estimates E in this case, is computed. It has been shown, that the standard deviation of such an estimate approximates the standard error of the statistic as if being sampled from the unknown population without replace-

ment (EFRON 1981, SOKAL & ROHLF 1995). For each value of the standard error 5000 runs of the bootstrap sampling were performed .

Tukey's jackknife method:

Let E be the estimated species number based on n samples and E_{-i} be the estimated species number ignoring the i th sample. Then a bias-corrected jackknifed estimate of the species number \hat{E} and of its approximate standard error $s_{\hat{E}}$ can be calculated as the mean and standard deviation of the so-called pseudovalues ϕ_i . Computation of the pseudovalues,

$$\phi_i = nE - (n-1)E_{-i}$$

of the jackknifed estimate of the species richness estimation,

$$\hat{E} = \frac{\sum \phi_i}{n} = \bar{\phi}$$

and of the approximate standard error.

$$s_{\hat{E}} = \sqrt{\frac{s_{\phi}^2}{n}} = \sqrt{\frac{\sum (\phi_i - \bar{\phi})^2}{n(n-1)}}$$

These estimated standard errors were compared with the real standard error, which can be calculated from the estimation results of the 1000 simulation repeats of each simulation run. The difference between this "true" standard error from the species richness estimates and the various estimated standard errors were used as a measure of quality from these estimates of standard error. The percentage difference between the "true" standard error and the mean estimates is called "percentage difference".

The accuracy and reliability of the species richness estimates is affected by the number (of incidences) of species records and the curve shape index (CSI, see Chapter 4.2.3 and 5.2.5). The standard error is a measure of the reliability of the estimates, hence, it can be assumed that its estimation is also affected by these factors. Thus, the performance of the estimators of standard error was analyzed in terms of the CSI and the number of species records as contour plots of the percentage difference fitted by the distance weighted least squares method.

The ranking of the different methods of estimating the standard error was done in a similar way to that of the species richness estimates (see Chapter 5.2.5). However, the percentage difference (weight: 3) and the standard deviation of the estimates of standard error (weight: 2) were the measures of quality. The percentage difference was weighted higher because an increased difference between the estimated and the "true" standard error affects its usefulness more than an increased standard error. The weighted mean ranks were used to indicate which of the estimators of standard error was generally the most accurate one in the study.

6.3 Results

The estimators of standard error showed a different relative performance depending on the estimator of species richness they were used for. In all coverage estimators (*CoverX*) and in the moment estimator (*Moment*) the bootstrap estimator of standard error turned out to be most accurate and reliable

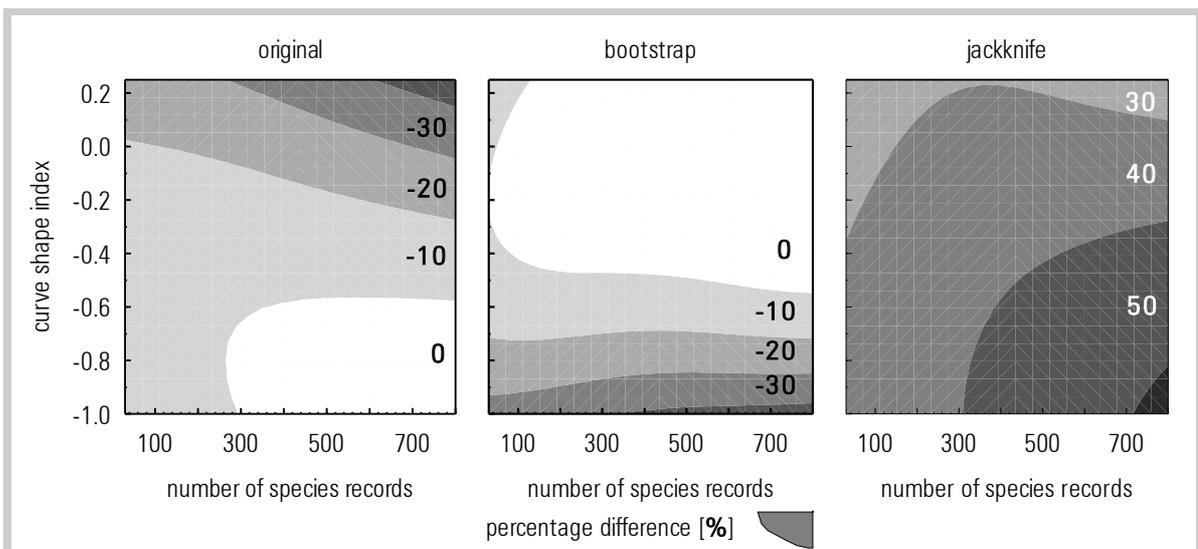


Fig. 49 Comparison of the performance by percentage differences of three estimators of the standard error of species richness estimates of *Cover1* in terms of the number of species records and curve shape index (CSI).

(Fig. 49). Nevertheless, the results of *Cover1* showed that the original estimator was the best performing one, if the CSI was low (< -0.6). Generally, in ranges of the number of species records and the CSI, where the original and the bootstrap estimator of standard error did not perform well, they underestimated the “true” standard error. In contrast, the jackknife method usually overestimated the standard error severely and, hence, was much less useful than the others for the *CoverX* estimators (Fig. 49) and *Moment*. In conclusion, the bootstrap method is usually the better one, however, the original estimator should be preferred, when the effort in the field is low, especially, when the number of species is high.

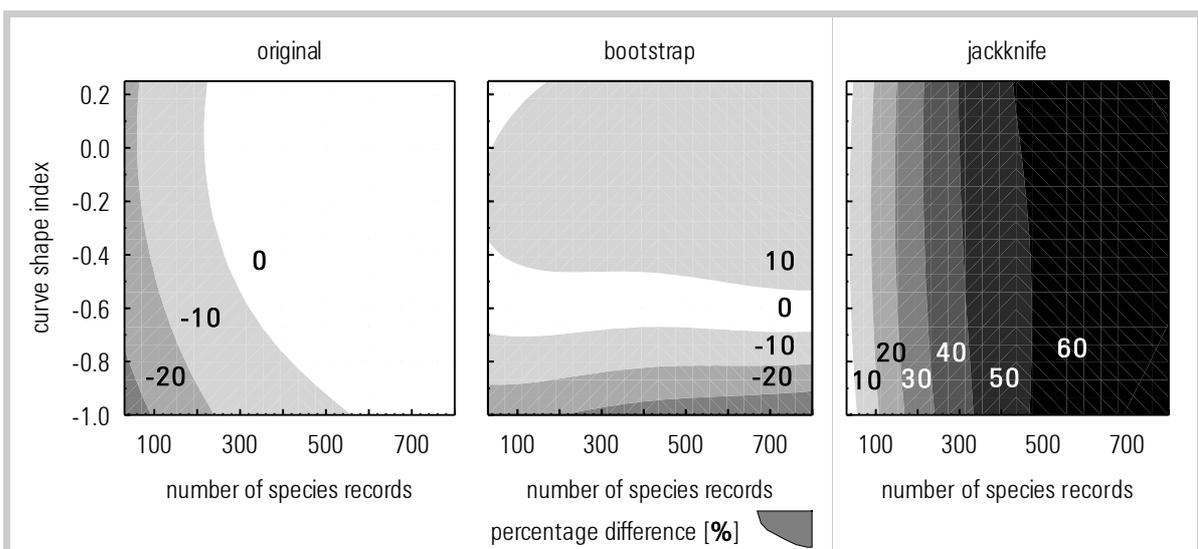


Fig. 51 Comparison of the performance by percentage differences of three estimators of the standard error of species richness estimates of *Jackknife1* in terms of the number of species records and curve shape index (CSI).

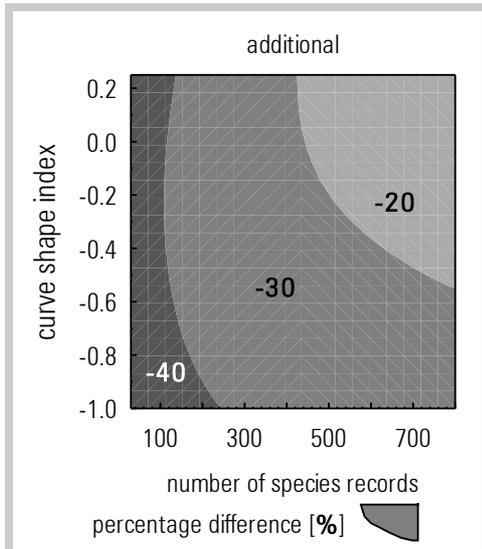


Fig. 50 Performance by percentage differences of the estimator of the standard error of species richness estimates of *Jackknife1* of HELTSHE & FORRESTER (1983) in terms of the number of species records and curve shape index (CSI).

In *Jackknife1*, the original estimator of standard error tended to underestimate the “true” standard error, when the number of species records was small (< 200) (Fig. 51). The bootstrap estimator tended to underestimate when the CSI was low (< -0.8). Both of these estimators of standard error were accurate and reliable in most of the ranges of number of species records and CSI, especially, in the ranges of good estimates of species richness of *Jackknife1* (see Chapter 5.3.3). The jackknife estimator of standard error again drastically overestimated the true standard error of the species richness estimates. The estimator of standard error suggested by HELTSHE & FORRESTER (1983) clearly underestimated the “true” standard error of the species richness estimates (Fig. 50).

For the species richness estimates of *Jackknife2*, the original estimator of standard error was very accurate in a wide range of number of species records and CSI (Fig. 52)

. It only slightly underestimated in the case of small numbers of species records. The bootstrap method of estimating the standard error tended to underestimate slightly when the CSI was low and the number of species records was high. It tended to slightly overestimate in the case of low CSI values. The jackknife method for estimating the standard error again severely overestimated the true values. In conclusion, the original as well as the bootstrap estimator of standard error can be used to

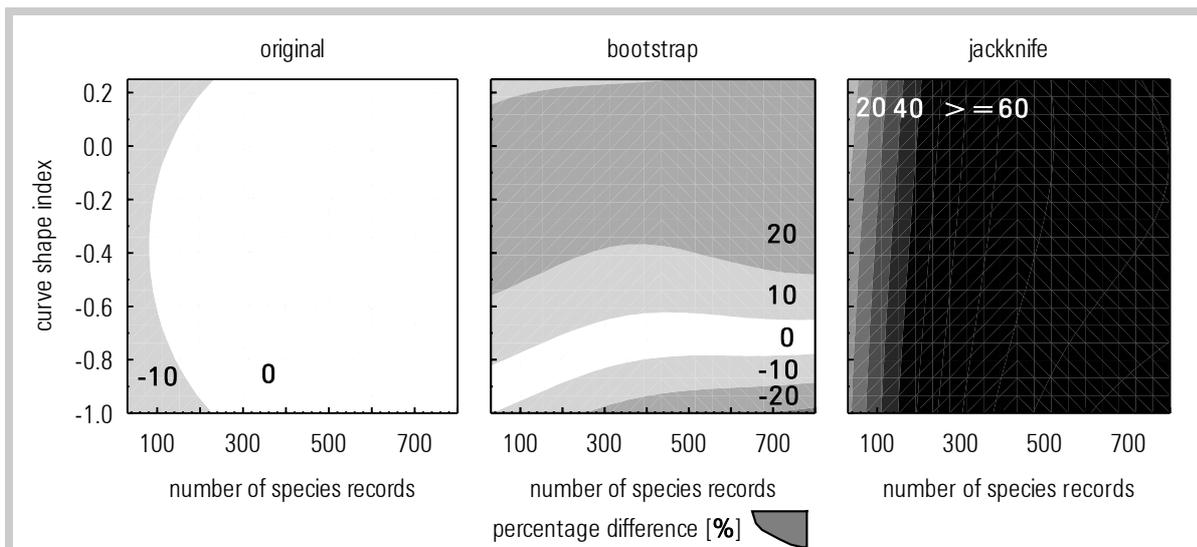


Fig. 52 Comparison of the performance by percentage differences of three estimators of the standard error of species richness estimates of *Jackknife2* in terms of the number of species records and curve shape index (CSI).

estimate the standard error of the species richness estimates of *Jackknife1* and *Jackknife2*.

Table 6 summarizes the performance of the estimators of standard error for the studied estimators of species richness. In the *CoverX* estimators of species richness, the bootstrap method always reached the most accurate and reliable estimates. For *Moment* it was the same. In *Jackknife1* the original and the bootstrap method of estimating the standard error were very close with some advantages for the original method. The method of HELTSHE & FORRESTER (1983) did not achieve the same accuracy. In *Jackknife2* the original estimator of standard error was the most accurate and reliable. However, the bootstrap method was also useful. The jackknife method for estimating the standard error of species richness estimates always clearly overestimated the "true" standard error, hence, it should not be used for this purpose.

Tab. 6 Ranks of the estimators of standard error for each of the species richness estimators show which is the recommendable.

	original	Jackknife	Bootstrap	extra
Cover1	2	3	1	
Cover2	2	3	1	
Cover3	2	3	1	
Cover4	2	3	1	
Cover5	2	3	1	
Cover6	2	3	1	
Moment	2	3	1	
Jackknife1	2	3	1	4
Jackknife2	1	3	2	

6.4 Discussion

Though estimators of species richness were compared in several studies, the corresponding estimators of the standard error were hardly ever evaluated. Moreover, some authors proposed to use alternative nonparametric estimators of standard error, the bootstrap method (CHAO ET AL. 1996, NICHOLS ET AL. 1998B, CHAO ET AL. 2001) and Tukey's jackknife method (MANLY 1977). A useful comparison of the original and the nonparametric estimators of standard error requires "true" values for the standard error. The simulation study with its 1000 simulation runs of virtual sampling in the same community with the same method and the same size of heterogeneity enabled the calculation of such "true" standard errors. Thus, the simulation study provided the basis to compare these estimators of standard error for species richness estimates.

With powerful computers available, the computational requirements of the bootstrap technique is no longer an obstacle. In this study, it clearly demonstrated advantages. Thus, the assumption of its usefulness for estimating the standard error of species richness estimation (CHAO ET AL. 1996, NICHOLS ET AL. 1998B, CHAO ET AL. 2001) is confirmed. The general suitability of the original estimators of standard error developed for particular estimators of species richness (BURNHAM & OVERTON 1978, CHAO 1984, CHAO ET AL. 1992, CHAO & LEE 1992, OTIS ET AL. 1978) could also be shown. The alternative estimator of standard error for the first order jackknife (HELTSHE & FORRESTER 1983) delivered worse results and, hence, can not be recommended. The formula for the calculation of the standard error provided for *Jackknife2* by BURNHAM

& OVERTON (1978) could be interpreted in two ways (compare Appendix). Both were analyzed in this study. One of them has been used in their examples (BURNHAM & OVERTON 1978). This one performed very well (Fig. 52), and even slightly better than the bootstrap procedure, whereas the other one (Fig. 53) accurately estimated the standard error only in cases of low numbers of species records and a high CSI.

Tukey's jackknife method was reported to be useful in estimating the standard errors of estimated population parameters like the survival rates of insects at various stages and the duration of these stages (MANLY 1977). EFRON (1981) analyzed 15 estimators of the standard error for the Pearson's correlation coefficient as statistics of interest in a Monte Carlo experiment. Thus, the "true" standard error could be used to compare the performance of these estimators. In this study, the bootstrap estimator of standard error also performed best and the jackknife estimator also overestimated the "true" standard error, although only slightly. Therefore, it is surprising that Tukey's jackknife method clearly failed to accurately estimate the standard error of species richness estimates in this study. The jackknife estimator of standard error has not yet been used in combination with estimates of species richness and it can not be recommended for the future either.

This study was mainly performed in order to analyze the usefulness of nonparametric methods to estimate species richness (see Chapter 5). In this chapter it could be shown that the number (of incidences) of species records and the curve shape of the distribution of species' recording frequencies (CSI) also affect the performance of the estimators of standard error. However, the estimators of standard error originally developed for specific estimators of species richness and the bootstrap method of estimating the standard error are almost equally accurate and reliable under most conditions. As the bootstrap estimation of the standard error can be used with all estimators of species richness (see Chapter 5), its estimates are comparable between the different methods of estimating species richness. Thus, the proposition of CHAO ET AL. (2001) to generally use the bootstrap procedure to estimate the standard errors of species richness estimates is confirmed by this study.

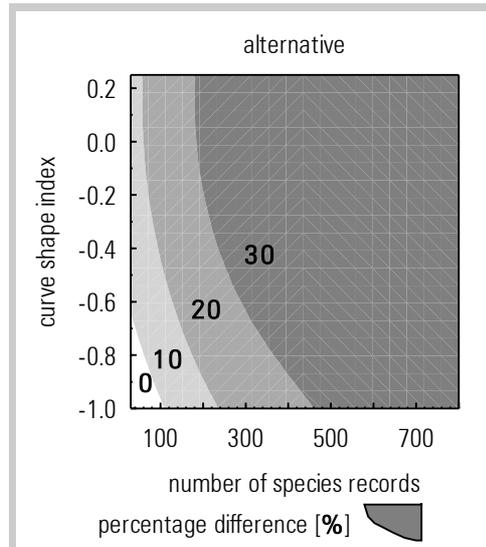


Fig. 53 Performance by percentage differences of one estimator of the standard error of species richness estimates of Jackknife2 of BURNHAM & OVERTON (1978) in terms of the number of species records and curve shape index (CSI).

7 Species richness estimators compared by means of field data

7.1 Introduction

In several species inventories not only the number of species was analyzed, but also the usefulness of several species richness estimators (e.g. BOULINIER ET AL. 1998, WALTHER & MORAND 1998). Most of these studies are based on only one data set of a single species group. In the RIVA project (SCHOLZ ET AL. 2001) four species groups were sampled with a design, which provides the opportunity to combine the data of the recorded species in a variety of ways. In this way it can be studied how the species group, the trapping effort, and heterogeneity in the spatial and temporal samples affect the results of different species richness estimators.

Accuracy and reliability of the estimators are not directly affected by these factors, but via statistics which the estimators are based on. The simulation showed that the number (of incidences) of species records and the distribution of species' recording frequencies, expressed here as the curve shape index (CSI, see Chapter 4.2.3), are the main parameters affecting the accuracy and reliability of the estimators (see Chapter 5). Their interaction is shown in Figure 54. The number of species records and the CSI can be derived from each data set of field data. Hence, it is possible to compare species richness estimators based on data from the field using these two parameters and to interpret the patterns of their results in the light of the simulation (see Chapter 5.3). Moreover, this confirms the rules for selecting an estimator (see Chapter 5.3.4).

The field data of the RIVA project on epigeal spiders, carabid beetles, molluscs, and plants offer wide ranges of mobility, species numbers, recording methods, and reactions to different environmental factors. Hence, all kinds of temporal and spatial heterogeneity affect species recordings more or less and, consequently, the number of species records and the CSI. Thus, the field data provide examples of wide ranges of these parameters.

The aim of this chapter is to show based on examples of field data that the species richness estimators show stable patterns of results from their species richness estimates depending on the number of species records and the CSI. This is discussed in the light of the patterns of precision and reliability of the estimators depending

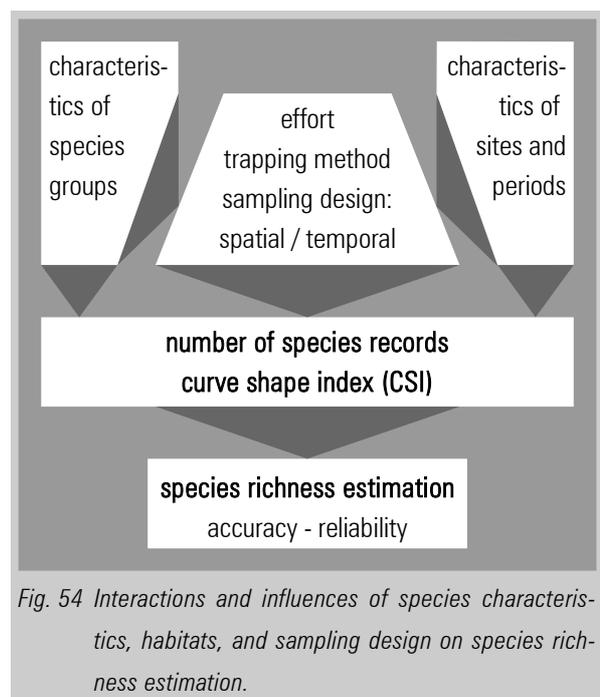


Fig. 54 Interactions and influences of species characteristics, habitats, and sampling design on species richness estimation.

on these parameters found in the simulation (see Chapter 5).

7.2 Methods

The study design of the RIVA project enables the estimators to be applied to a huge number of data sets, which are very different in their number of species records and their CSI.

For this investigation, four species groups investigated in the RIVA project are used, carabid beetles, molluscs, plants, and epigeal spiders (see Chapter 3.2). These species groups were recorded on 36 study sites, which could be divided into ecologically homogeneous groups that can be used as spatial samples for estimation. Additionally, single traps and single soil samples provide samples for site specific estimates for carabid beetles as well as for epigeal spiders and molluscs respectively. For carabid beetles and plants, data from six study periods over two years were available and they were used as temporal samples. The four study periods available for molluscs are too few to be used for temporal species number estimation. Additionally, sampling was carried out for epigeal spiders and carabid beetles for three study periods with eight two-day sampling periods. These are used for temporal estimates during single study periods.

This variety of spatial and temporal sampling makes it possible to get a wide range of values for the number of species records and the CSI. In the RIVA project field data, the values from the number of species records (Ncap) cover a range from about 30 to more than 1000 and the values of the CSI cover a range from nearly +1 to nearly -1. Dividing these ranges into three sections, i.e. < 100 , $100 - 500$, and > 500 number of species records and < 0.0 , $0.0 - 0.5$, and > 0.5 of the CSI, results in nine quadrants defined by the ranges of numbers of species records and the values of the CSI, which can be illustrated by examples from the field data. Moreover, this provides sets of examples, which are biologically interpretable in terms of effort, species group, as well as the spatial and temporal heterogeneity of samples. Hence, these examples make it possible to show the coherence between the above factors and the pattern of estimates of the studied estimators.

These are six estimators based on the concept of coverage, *Cover1*, *Cover 2*, *Cover3* (CHAO ET AL. 1992), *Cover4*, *Cover 5*, (CHAO & LEE 1992), and *Cover6* (CHAO & LEE 1993), a moment estimator *Moment* (CHAO 1984), two jackknife estimators *Jackknife1* and *Jackknife2* (BURNHAM & OVERTON 1978). More details can be found in Chapter 5.2.3 and in the Appendix. Four estimators proved to work best in the simulation: *Cover1*, *Cover3*, *Jackknife1* and *Jackknife2* (see Chapter 5.3). These are compared with selected field data to exemplify the effects of effort, of characteristics of the species groups, and of spatial and temporal heterogeneity on the number of species records and the CSI and, hence, the performance of the estimators .

For all estimators of species richness the bootstrap estimator of standard error was used because it proved to work well (see Chapter 6.3) and is comparable between the estimators of species richness.

The error ranges given from the estimates are constructed by adding and subtracting the estimated standard error respectively.

7.3 Results

A comparison of the numerous data sets from the field showed stable patterns of results of the species richness estimators in terms of number (of incidences) of species records and CSI. These patterns of differences in the estimates of all estimators are presented in terms of typical examples for different ranges of the number of species records and the CSI. The wide range of values of sampling effort, characteristics of the species groups, and differences among sites and periods in the field data enabled the complex effects of these factors to be shown on the patterns of results from species richness estimators. Selected examples from the field data showed for those estimators, which were most precise and reliable in the simulation (see Chapter 5.3), that the number of species records and the CSI are more useful predictors of the best estimators than the available knowledge on the affecting factors.

7.3.1 Estimates relating to the number of species records and curve shape index

Generally, in examples with high numbers of species records (Fig. 55f,i) or a very high value of the CSI (Fig. 55a) most of the estimates of species richness were relatively similar and the estimated ranges of the standard error were relatively small. It can be assumed for these examples, that most of the estimators matched the "true" numbers of species quite well, especially, because all examples were selected using the criteria of preferably showing differences between estimates.

Three of the coverage estimators, *Cover1*, *Cover2*, and *Cover3*, resulted in very close estimates of species numbers (Fig. 55) in all examples. *Cover4* and *Cover6* always estimated smaller numbers of species, although still within the range of the standard error of the other coverage estimators. This pattern did not show any coherence with the CSI or the number of species records. In many cases, the estimates of *Cover5* were the highest among the coverage estimators and the difference increased with decreasing values of the CSI (Fig. 55g,h,i).

The estimates of *Jackknife1* were usually close to that of *Cover1*, *Cover2*, and *Cover3* in all examples (Fig. 55). However, they were comparably low when the CSI was low and the number of species records was low (Fig. 55d,g) and the other way round (Fig. 55b,c). *Jackknife2* often provided high estimates (Fig. 55). Except when the number of species records was low, *Jackknife2* had to be assumed to overestimate the "true" number of species. *Jackknife2* usually overestimated the standard error. It even estimated species numbers, which were lower than the recorded number of species ($D = 14$), when the CSI was high and the number of species records low (Fig. 55a).

The *Moment* estimator showed a lack of reliability. Sometimes it estimated much higher species

numbers than the other estimators (Fig. 55b,e) and sometimes it even gave no result (Fig. 55d). In most cases its estimated standard error was very high.

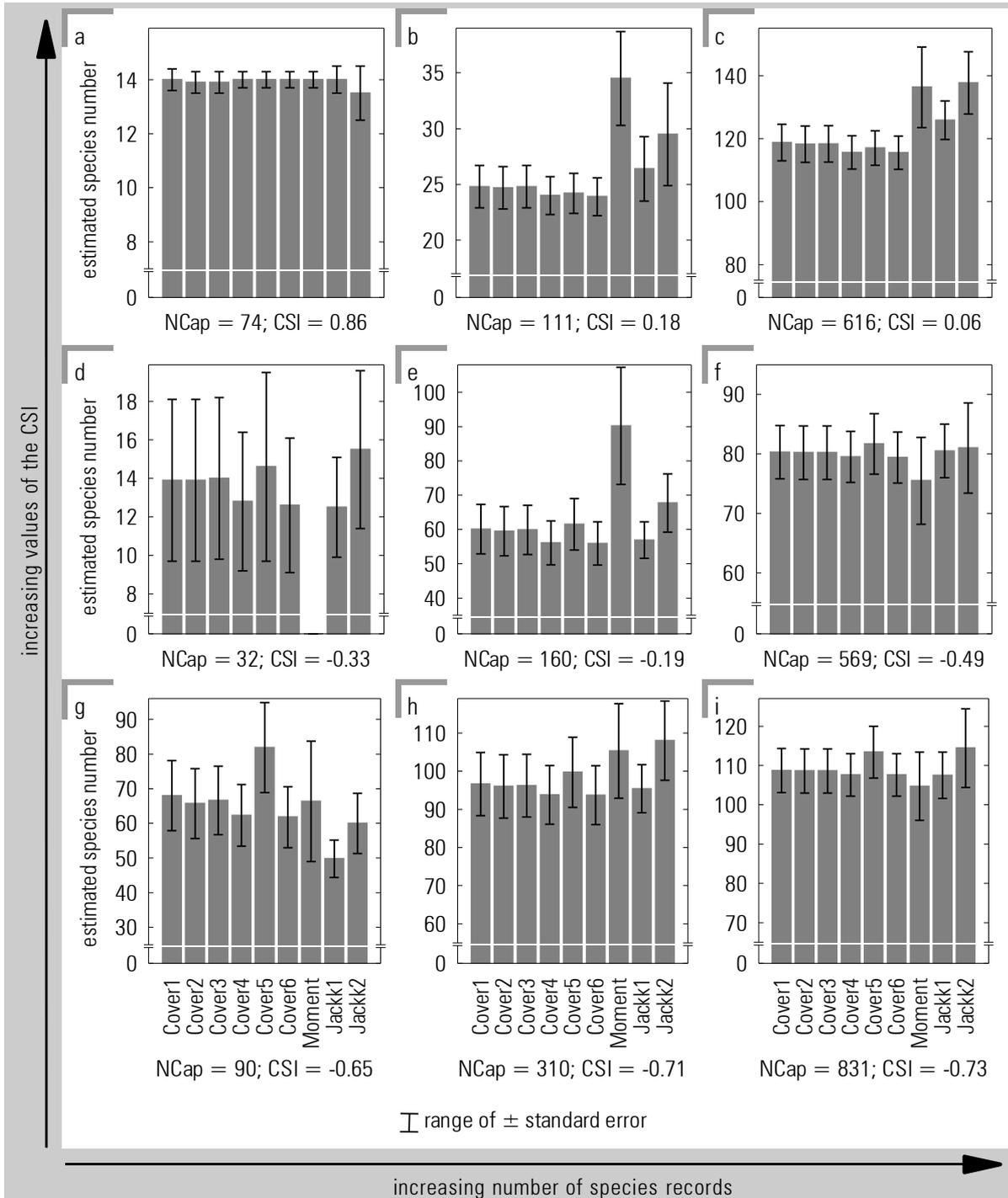


Fig. 55 Comparison of the estimates of species numbers of nine different estimators for different numbers of species records (NCap) and values of the curve shape index (CSI). The standard error ranges were calculated with the bootstrap method.

7.3.2 Effort and species group

Different aspects of the effect of increasing effort are presented using one example from the molluscs (Fig. 56) and two examples from the carabid beetles (Fig. 57, 58). The mollusc data originate from a homogeneous group of study sites with five soil samples each. The points on the curves represent the means of estimates based on an increasing number of soil samples.

In the studied habitats, the number of mollusc species was small compared to the other species groups. The increase in the number of species records and of the CSI became smaller the more soil samples had already been used for the estimate (Fig. 56). This is confirmed by the rapidly decreasing difference between the recorded and the estimated number of species. Therefore, in this example the effort was

most probably high enough to have recorded nearly all the mollusc species. Although the relative position of the estimates did not change, the ranges of the estimated standard error decreased with an increasing effort except that of *Jackknife2* (Fig. 56). This shows that in this example *Jackknife2* most probably provided an accurate estimate with just a few samples, however, reliability was lowest.

The curves of the example from the carabid beetles resulted from the same procedure, which was performed with the soil samples for the molluscs, however, with the estimates being based on traps (Fig. 57). Thus, increasing effort in this example means an increasing number of traps per site. The estimation was performed using the same samples spatially and temporally. In both cases the CSI and the number of species records increased with increasing effort (Fig. 57a,b). The number of recorded species as well as the number of estimated species increased, too. The curves of the estimates became clearly flatter to the right. This is an indication that the estimates of the accurate estimators were close to the "true" number of species. This results only, if the increasing effort does not introduce too much additional heterogeneity and, therefore, new species. Especially, in the spatial sampling (Fig. 57a), the patterns of results of the species richness estimators changed depending on the effort.

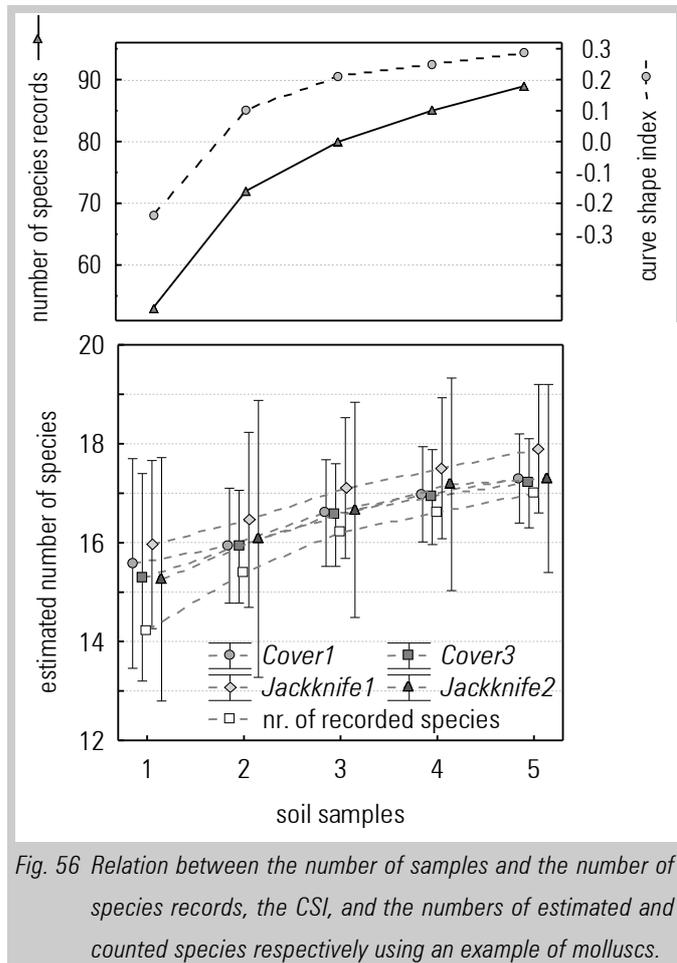


Fig. 56 Relation between the number of samples and the number of species records, the CSI, and the numbers of estimated and counted species respectively using an example of molluscs.

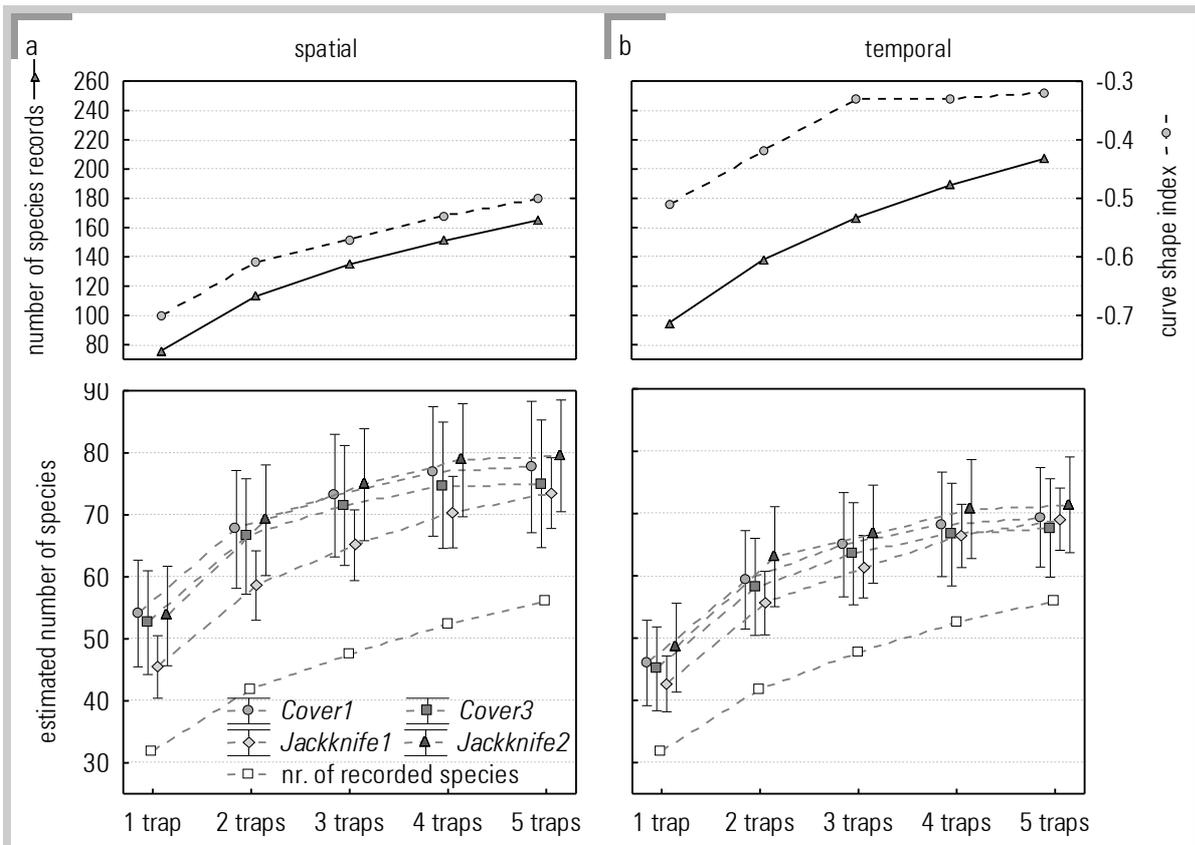


Fig. 57 Relation between the number of samples and the number of species records, the CSI, and the numbers of estimated and counted species respectively using the example of carabid beetles. The estimates are based on the same species records but used as spatial (a) and temporal (b) samples respectively.

When the effort was low (one trap), *Jackknife1* showed the lowest estimates, however, it was quite close to the other estimators when using five traps.

Although the number of recorded species is the same regardless of using the samples spatially or temporally, the number of species records and the CSI were different. This caused the differences in the estimates. The higher CSI and the higher number of species records yielded slightly but regularly smaller estimates when using the samples temporally (Fig. 57b). This is an indication, that the temporal heterogeneity was smaller than the spatial one in this data set. This was confirmed by the smaller values of the estimated standard error in the temporal case.

The relation of effort and heterogeneity of samples and their effect on species richness estimates is presented by an example of data from carabid beetles sampled over six periods for two years (Fig. 58). The points on the curves represent the means of estimates based on an increasing number of periods. Although the CSI increased and the number of species records reached high values, the estimates increased continuously and did not seem to be close to a maximum level (Fig. 58). The ranges of the standard errors of the estimates increased with the increasing effort and the results of the different

estimators tended to diverge. Thus, an increasing effort, which means an increasing number of different study periods in this example, did not always result in more accurate and reliable estimates.

The following two examples were selected to present differences in the patterns of results of the estimators in relation to different species groups and their differences between sites. Thus, the effort of recording had to be similar for all compared species groups.

A comparison of the data from different species groups from similar groups of sites of the same habitat showed different numbers of species and different abundances in the field (Fig. 59). Consequently the species groups also differed in the numbers of species records (Ncap) and in the curve shape index (CSI). For the carabid beetles *Jackknife1* estimated the second highest species numbers, for the plants the lowest. The number of recorded species of carabid

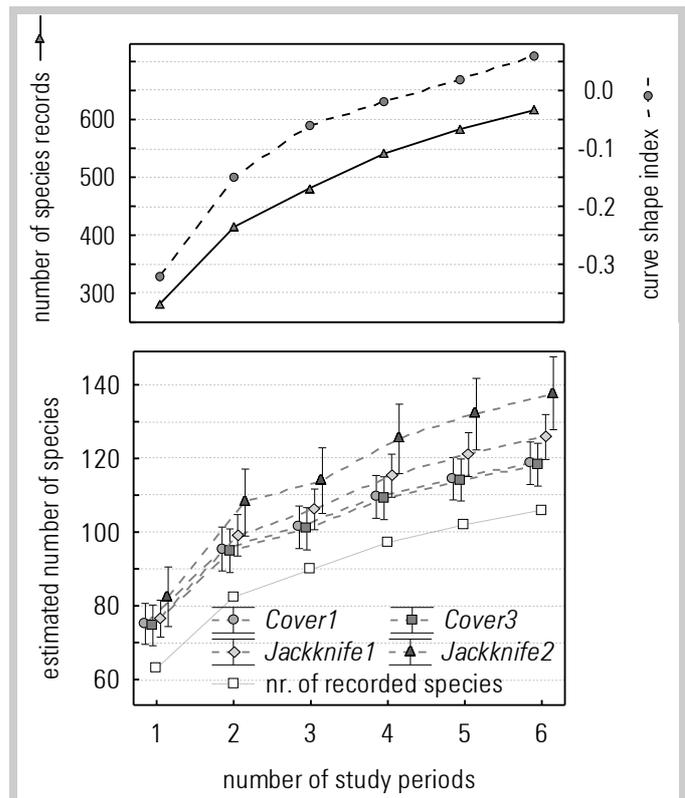


Fig. 58 Relation between the number of samples and the number of species records, the CSI, and the numbers of estimated and counted species respectively using the example of carabid beetles.

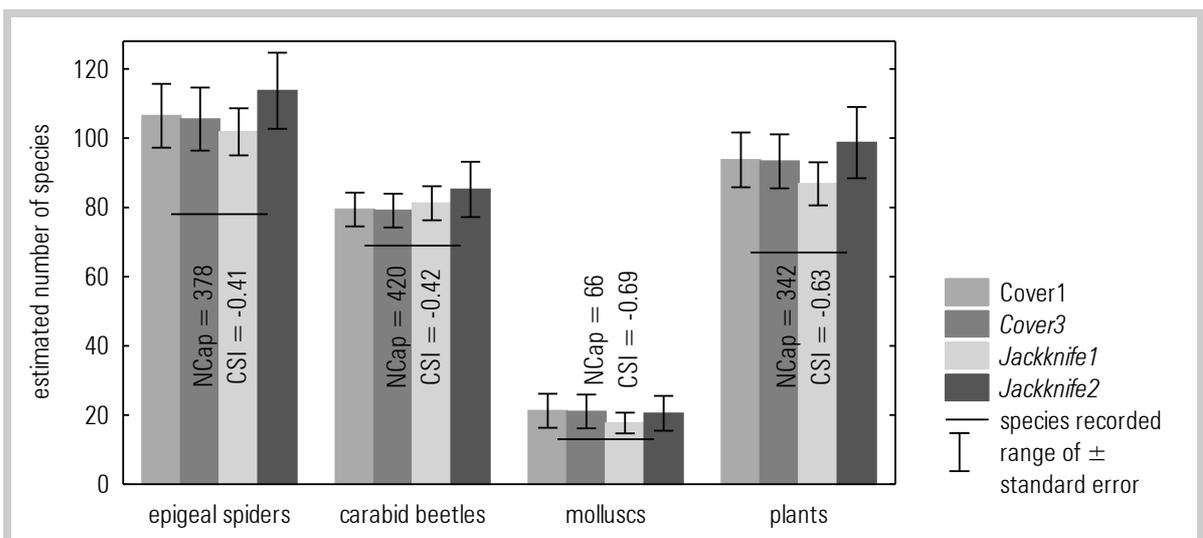


Fig. 59 Comparison of the patterns of results of species richness estimators with data from different species groups from similar sites collected with comparable effort.

beetles and plants were very close, whereas the values of the CSI and the number of species records (Ncap) were different. This caused the general differences in the estimated species richness of these two species groups and the difference in the sequence of the estimators (Fig. 59). The communities of molluscs and epigeal spiders displayed very different numbers of species. Nevertheless, the sequence of the estimators was similar. *Jackknife1* estimated the lowest. For all species groups the estimated standard error was the highest in *Jackknife2* (Fig. 59). Therefore it can be concluded that the numbers of recorded species is not a criteria as to which of the species richness estimators performs best.

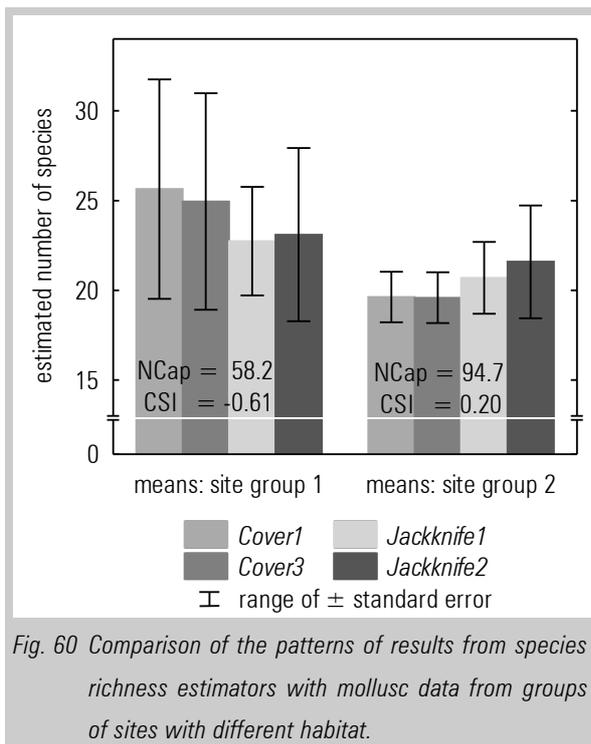


Fig. 60 Comparison of the patterns of results from species richness estimators with mollusc data from groups of sites with different habitat.

Neighboring sites in different habitats, can exhibit communities of the same species group with different species numbers and different abundances. Consequently, they can greatly differ in the number of species records (Ncap) and the CSI value. The mollusc data from two different groups of study sites exemplified this (Fig. 60) i.e. the patterns of results from the species richness estimators were different for the two site groups. Whereas for the site group 1 *Cover1* and *Cover3* estimated a higher species richness, for the site group 2 *Jackknife1* and *Jackknife2* did. Moreover the standard error ranges were much wider for the estimate based on site group 1 (Fig. 60). Therefore, the species group is not useful either to predict the best estimator for a certain data set from the field.

7.3.3 Effects of sampling design and heterogeneity of sites and periods

Carabid beetles were caught over three study periods over eight two-day-periods for each study period on eight homogeneous sites. This sampling scheme therefore provides species records for 24 temporal samples but only for eight spatial ones.

Even if the spatial and the temporal heterogeneity in the samples can be assumed to be similar, the way of using the trapping results affected the number of species records and the CSI and, hence, it affected the patterns of results of the estimators. In the spatial case, the estimates of *Cover1*, *Cover3*, and *Jackknife1* were very close (Fig. 61). In the temporal case, the estimates of *Cover1*, *Cover3*, and *Jackknife2* were close, whereas *Jackknife1* most probably slightly underestimated the "true" species number. The estimated standard error of the estimates from *Cover1* and *Cover3* was higher in the tem-

poral case than in the spatial one. Thus, grouping the same trapping data into different numbers of samples changed the results of the species richness estimators (Fig. 61).

This difference was mainly caused by the difference in the number of species records, because each species is recorded once in one sample ignoring the abundance of these species. Thus, using the same captures, the number of species records increases when the number of samples increases. The CSI decreased (Fig. 61), because few species were abundant enough to be recorded in many of the 24 temporal samples, whereas a number of them were present in all eight spatial samples.

Another effect from sampling design can be studied with field data, if inside a homogeneous group of sites the differences between the traps from one site are within a similar range to the differences between the sites. Epigeal spiders and carabid beetles were trapped with five traps on each study site. The field data provided 60 data sets from

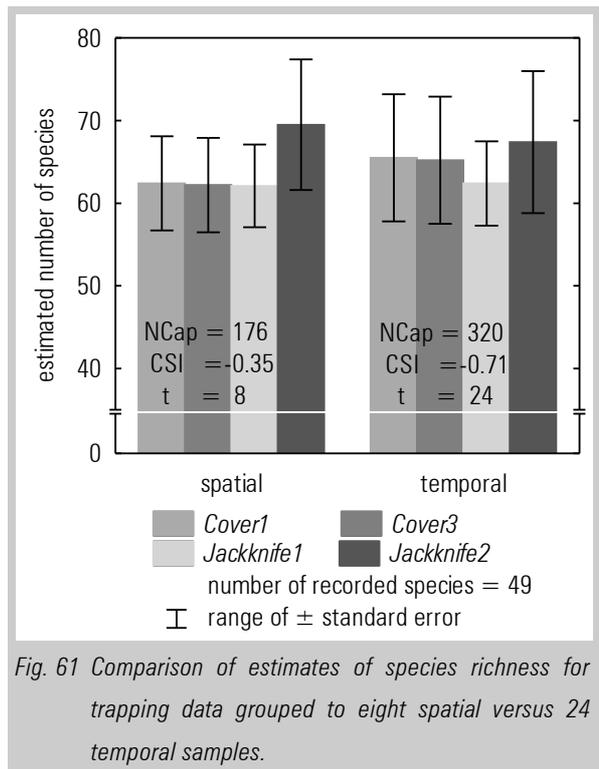


Fig. 61 Comparison of estimates of species richness for trapping data grouped to eight spatial versus 24 temporal samples.

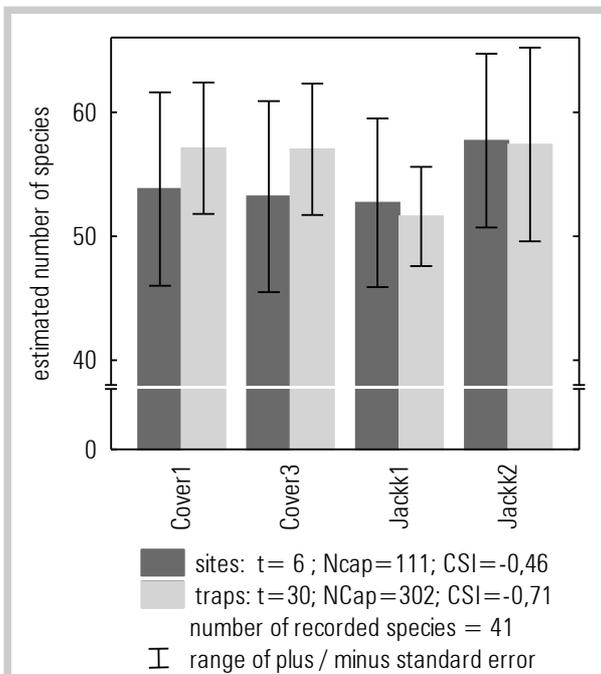


Fig. 62 Estimates of species richness based on trapping data from single traps compared to estimates based on the same data pooled for sites.

epigeal spiders and carabid beetles. These were used to test, whether the differences in the species richness estimates based on sites versus traps are significant for the different estimators using the Wilcoxon matched pair test. The differences of the estimates of the coverage estimators with sites versus traps as samples were all highly significant ($p > 0.0001$), whereas that of the jackknife estimators and of *Moment* were not. The species richness estimates of the coverage estimators are mainly based on the number of species records and the CSI, whereas the estimates of the jackknife estimators are mainly based on the number of samples and the first two recording frequencies. This obviously makes them differently sen-

sitive to differences in the sampling design.

In order to illustrate this, an example is presented (Fig. 62) in which the estimates of species numbers based on pooled data of the five traps of each site ($t = 6$) are compared to the estimates of species numbers based on the species records of the single traps ($t = 30$). Using the species records of the traps, resulted in clearly higher numbers of species records and a clearly lower CSI than using the trapping results from the whole sites (Fig. 62). When the species records from the traps were used as a basis for species richness estimation, the estimates were higher in *Cover1* and *Cover3*, but similar in *Jackknife1* and *Jackknife2*. The difference in the number of samples (t) hardly affected the estimates of the jackknife estimators, although t plays a major role in their formulas. As the number of species records and consequently the CSI were different and in the coverage estimators the number of species records and all recording frequencies are used for the estimation, these estimators were af-

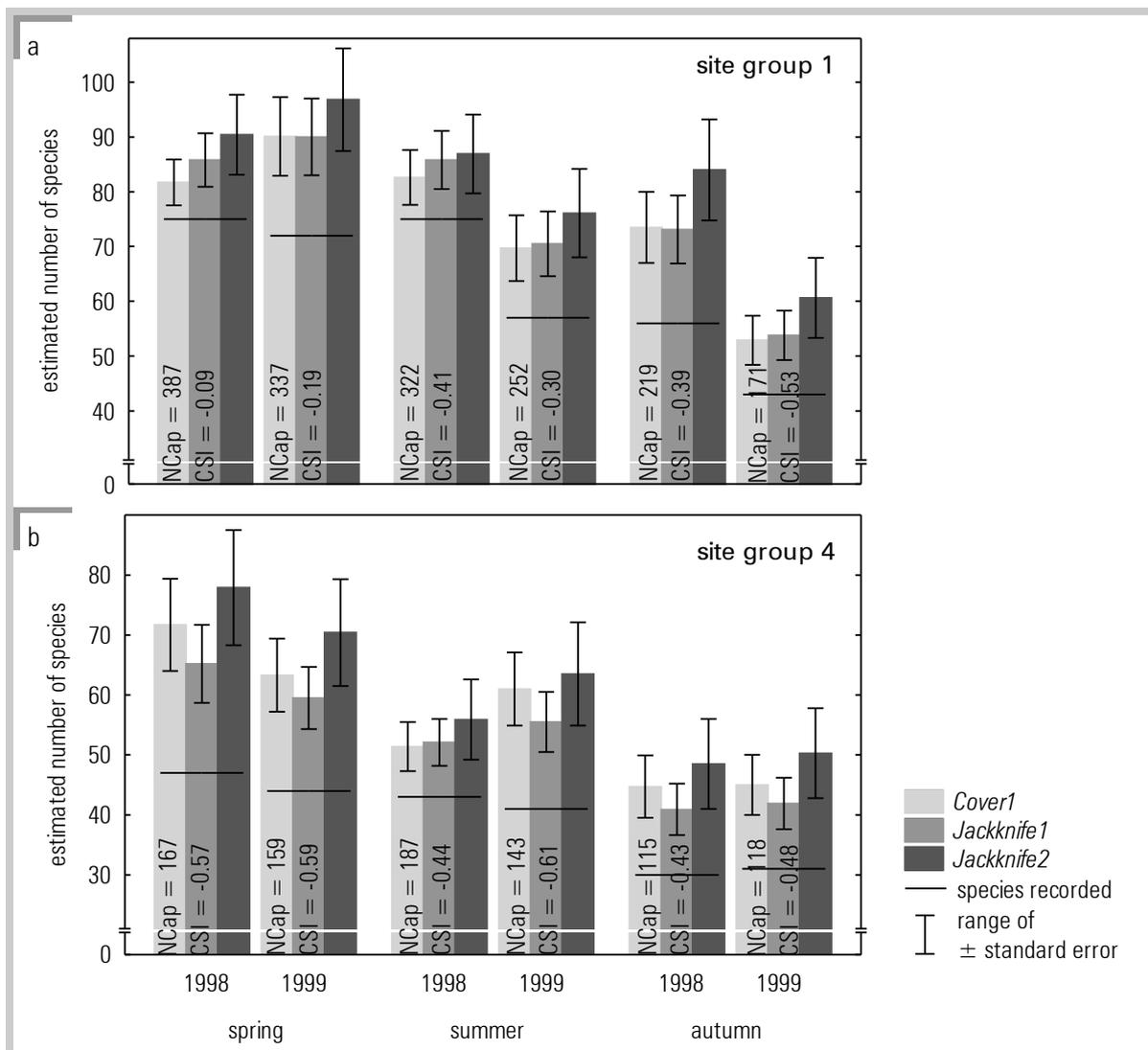


Fig. 63 Comparison of the patterns of results from three estimators in terms of the number of species records and CSI for different periods and years from one moist (a) and one dry (b) group of sites.

ected more strongly. With the exception of *Jackknife2*, the estimated standard error was clearly smaller when using the species records of the traps as samples (Fig. 62). The patterns of results from the estimators in terms of different sampling designs in the examples above showed, that the sampling design is not a good criterion for selecting the best estimator.

It became obvious from the field data that sampling sites and sampling periods over a year as well as between years provided different numbers of recorded species. Effects of this heterogeneity in the samples on the patterns of results for the species richness estimators are represented by two examples of temporal heterogeneity in carabid beetles and an example of a comparison between the spatial and the temporal heterogeneity in carabid beetles versus plants.

The number of species records and the CSI of the data from carabid beetles varied from study period to study period and from year to year without an obvious rule (Fig. 63a). Furthermore, the study periods were different for different sites. Whereas for site group 1 (moist sites) in the summer and in the autumn of 1998 the recorded as well as the estimated number of species was clearly higher than in 1999 (Fig. 63a), for site group 4 (dry sites) they were similar (Fig. 63b). For site group 1, the number of species records was quite similar for all periods of 1998 but different in 1999 (Fig. 63a), whereas for site group 4 the periods were similarly different in both years (Fig. 63b). When the CSI was lower than about -0.5, *Cover1* usually estimated higher species numbers than *Jackknife1*, however, when the CSI was higher than about -0.3 the opposite was the case. Thus, the year or period of recording is not useful in predicting the estimators' performance.

Jackknife2 again had the highest values for the estimated standard error.

Plants are not mobile, hence, most of the species can be recorded over the whole vegetational season and the species lists from different study periods are mostly the same. Thus, the temporal heterogeneity for the plant samples should be very small, whereas the spatial heterogeneity should be similar to both of the mobile carabid beetles. This is illustrated by an example of data from these species groups from the same sites.

The relative difference (spatial/temporal) in the number of species records (Ncap) was small (14% of the smaller Ncap) for the carabid beetles and high (84% of the smaller Ncap) for the

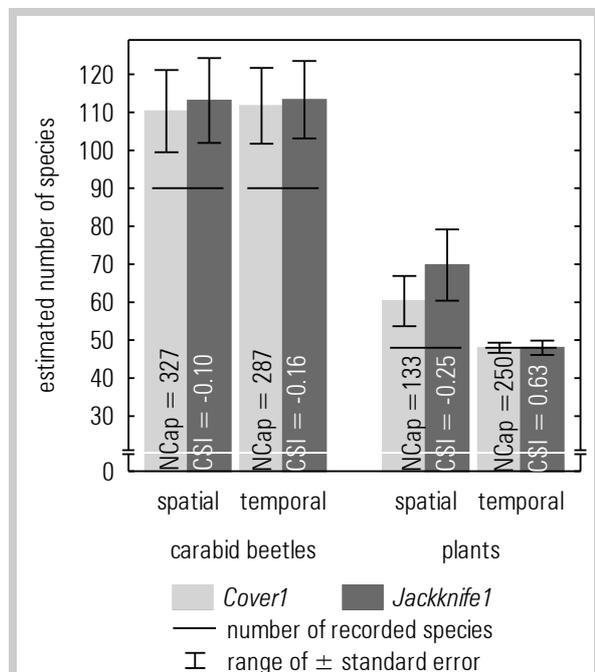


Fig. 64 Comparison of the estimates in terms of the number of species records and CSI for spatial versus temporal samples of two species groups from the same sites.

plants. The CSI was similar for carabid beetles and very different for the plants (Fig. 64). As the numbers of periods (6) and sites (7) used for the plants were similar, the differences in the number of species records and the CSI must be an effect of the differences between spatial and temporal heterogeneity. Hence, the estimates and their estimated ranges of standard error based on spatial versus temporal use of the records were different for the plants but similar for the carabid beetles. For the plants the temporal samples consisted of nearly identical species. Therefore, the number of counted species was also the number of estimated (Fig. 64).

7.4 Discussion

7.4.1 General discussion

Generally speaking, increasing effort resulted in increasingly similar species richness estimates (Fig. 57, COLWELL & CODDINGTON 1994), which means, that the estimates converge to the "true" number of species. If the estimated and the counted numbers of species do not become more similar with increasing effort it must be assumed that the samples originate from temporally (Fig. 58) or spatially (CODDINGTON ET AL. 1996, TOTI ET AL. 2000) heterogeneous samples. This can indicate that even high effort is not enough to completely sample a species community, for example the spider community of the Appalachians (CODDINGTON ET AL. 1996, TOTI ET AL. 2000), or that a community is not closed in terms of temporal movements of mobile species in the spatial scale of the sampling, for example carabid beetles in floodplains (Fig. 58).

PALMER (1990) assumed for his data set of plants, that the communities did not change over his sampling period of three years. This was also found in this study (Fig. 64). Therefore, using the homogeneous temporal samples, the estimates only account for those species, which were overlooked by reasons of seasonal recordability of plant species, however, not for those species, which were overlooked because of variability inside the study area. Thus, if it is intended to estimate the number of plant species of an area, that were not recorded on the sampling sites over a number of sampling periods, the heterogeneous spatial samples have to be used for estimation. This means that the differences in the samples must reflect the variability in the recordability of the species, whether this be spatial or temporal, which is the reason for estimating species richness.

Former studies focused on single species groups like parasites (WALTHER & MORAND 1998), spiders (DOBYNS 1997, TOTI ET AL. 2000), plants (PALMER 1990), or birds (BOULINIER ET AL. 1998) as well as on scales like the whole Appalachians (CODDINGTON ET AL. 1996, TOTI ET AL. 2000) or the Brunei tropical forest (MAWDSLEY 1996). In contrast this study is based on a small scale and four species groups (SCHOLZ ET AL. 2001) of which two apparently have not been used for species richness estimation before. As the number of species records and, the CSI in particular are not reported in these studies, their species rich-

ness estimates can not be interpreted in terms of these two factors. Nevertheless, the patterns of results from the estimators in such papers can be compared with the results of this study. The study design which was used to collect the field data for this study, provided a huge number of data sets. The examples of Figure 55 demonstrate general patterns of results from the estimators, which were found in the estimates based on these data sets. At least some of the estimators which were compared in this study were previously investigated in some recent papers.

Jackknife1 generally estimated lower numbers of species than *Jackknife2* (e.g. PALMER 1990, PALMER 1991, WALTHER & MORAND 1998). COLWELL & CODDINGTON (1994) showed that this results in a smaller bias of *Jackknife2* if the number of samples is small. As a small number of samples usually means a small number of species records, the pattern of results from *Jackknife1* and *Jackknife2* is equivalent to that in Figure 55. *Moment* showed little bias (WALTHER & MORAND 1998, TOTI ET AL. 2000) but was only a little reliable (COLWELL & CODDINGTON 1994, CODDINGTON ET AL. 1996). This is also obvious in the examples of Figure 55 because *Moment* showed a comparably high standard error and some outliers. COLWELL & CODDINGTON (1994) and TOTI ET AL. (2000) used *Cover4* and *Cover5* in their comparison of species richness estimators and reported that these estimators clearly overestimate, especially, *Cover5* with small numbers of samples. This was only confirmed for *Cover5*. Generally, the patterns from results of the estimators studied in these papers corresponded to the results of this study.

The data sets on which the comparisons of species richness estimators were based in the papers cited above were collected with different effort and from different species groups. However, for comparable ranges of the number (of incidences) of species records and the CSI, the patterns of results from the four estimators studied was similar to that in Figure 55 with examples of different effort (Fig. 56, 57) and of different species groups (Fig. 59, 60). Thus, effort and species group are not good criteria for predicting the performance of certain species richness estimators, but the number of species records and the CSI are.

BOULINIER ET AL. (1998) showed that differences between sampling sites in the general recordability of the species occur. In this study too temporal differences between sampling seasons occurred (Fig. 61, 63). Moreover, differences in the sampling design, the use of a small number of groups of traps as samples versus a high number of single traps for example, affect the patterns of results of the species richness estimators (Fig. 62). The examples based on field data in Chapter 7.3.2 and 7.3.3 mainly showed the same patterns of results for species richness estimators in terms of the number of species records and the CSI as those of Figure 55. Moreover, the patterns of results of the estimators studied in the papers above correspond to the results shown in Figure 55. It can therefore be concluded that the number of species records and the CSI are useful in predicting the best estimator for a set of field data, whereas factors like effort, species' characteristics, heterogeneity of samples, or sampling design are not.

7.4.2 Estimates based on field data in the light of the simulation

In species richness estimates from field data, the “true” number of species is not known. However, these estimated species numbers can be interpreted in light of the results from the simulation (see Chapter 5.3). It is known from the simulation how, for example, sampling effort or heterogeneity of spatial or temporal samples affect the number of species records and the CSI, which reflects the curve shape of the distribution of species' recording frequencies. It is also known from the simulation how this affects the results of the species richness estimates of different estimators (see Chapter 5). These patterns of effects can also be identified in estimates from field data. Former studies worked with one species group, at most resulting in a few data sets of sites or efforts, and no comparison of spatial and temporal sampling (e.g. SOBERÓN & LLORENTE 1993, CODDINGTON ET AL. 1996, NICHOLS ET AL. 1998A, WALTHER & MORAND 1998, SKOV & LAWESSON 2000). The data set used here (SCHOLZ ET AL. 2001) could be combined to numerous useful samples (see Chapter 3.2.3), which cover a wide range of number of species records and CSI. This offers extraordinary possibilities to interpret the estimates based on field data in light of the results from the simulation.

The general patterns of results from the species richness estimators found in the examples in the nine quadrants defined by the ranges of numbers of species records and values of the CSI (Fig. 55) also appear in the simulation (see Chapter 5.3.3). The simulation showed that all estimators underestimate the “true” species richness when the number of species records and the CSI are low. Moreover, it showed that *Jackknife1* has a stronger tendency to do this than the coverage estimators. In the examples covering these ranges of the number of species records and the CSI, *Jackknife1* estimated clearly lower species numbers than the coverage estimators. In the other cases, *Cover1*, *Cover3* and *Jackknife1* estimated quite similar numbers of species. The estimates of *Moment*, *Cover5* and *Jackknife2* were sometimes higher, sometimes lower than those of the best estimators and mostly had higher estimated standard errors. The simulation also showed that these estimators do not give very reliable results. Moreover, the simulation showed that *Cover2*, *Cover4* and *Cover6* underestimate the species richness a lot more than the best estimators. The estimates based on field data of these estimators were always lower than those of the best estimators. It can therefore be concluded that with the field data *Cover2*, *Cover4* and *Cover6* also underestimated the “true” species number a lot more than the best estimators.

Generally speaking, the effects of increasing effort are that the number of species records increases, the CSI increases, the accuracy and reliability of most estimators improve, the estimates become more similar, and the standard errors decrease. This is the usual pattern in the field data (Fig. 56) as well as in the simulation (see Chapter 5.3.2). However, there were exceptions. If the number of species records rapidly increases, whereas the CSI only moderately decreases, and the estimates of the different methods diverge with increasing effort (compare Fig. 58), the simulation suggests that the hetero-

geneity of the samples must be high. This can mean, that the effort is much too low to cover the variability of the sampled area or period, or that the sampled community was not closed. Moreover, the heterogeneity of samples can differ strongly depending on them being drawn spatially or temporally (Fig. 57 61, 64). This results in a different number of species records and CSI, and, hence, in different patterns of results from the estimators. However, no estimator can account for heterogeneity in its estimates, which is not covered by the samples. Thus, a sampling design, which excludes heterogeneity, which is responsible for the small recording probabilities of some species, is not useful when trying to estimate the number of species, which are probably overlooked because of this heterogeneity combined with limited effort.

When designing a field study, it sometimes has to be decided whether to collect lots of small samples (one trap, small plot) or a few larger samples (series of traps, large plot). For example, using 40 single pitfall traps instead of eight series with five traps each introduces extra sampling heterogeneity, if the study sites are not perfectly homogeneous, which is usually the case. In the field data example (Fig. 61) as well as in the simulation (see Chapter 5.3.2) a higher number of samples based on a lower number of combined traps resulted in higher numbers of species records and a higher CSI. The different effects on the estimates of *Jackknife1* and *Jackknife2* compared to *Cover1* and *Cover3* are caused by differences in their concept of estimating species richness. The patterns of results from the species richness estimators in terms of the number of species records and the CSI is again the same in the examples from the field as in the simulation.

From the examples of estimates based on field data interpreted in light of the simulation, it can be concluded that neither the species group itself nor parameters like spatial or temporal sampling design, assumed heterogeneity of samples, or a certain effort, give some indication as to which of the species richness estimators will be most accurate and reliable. Contrary, the number of species records and the distribution of the recording frequencies expressed as CSI are close to the statistics and easy to calculate from the field data. Moreover, the patterns of results of the estimators found in the simulation (see Chapter 5.3) confirm those with the field data. Consequently, the number of species records and the CSI are useful criteria for choosing the best possible method of estimating species richness from given field data.

8 Discussion

8.1 Comparison of species richness estimators

When BUNGE & FITZPATRICK (1993) stated a lack of studies comparing the methods of estimating species richness only a few studies had touched on the subject (SMITH & VAN BELLE 1984, PALMER 1990, 1991, BALTANÁS 1992). Since then, most of the comparisons of species richness estimators have been based on field data from single species groups (e.g. SOBERÓN & LLORENTE 1993, SOLOW 1994, CODDINGTON ET AL. 1996, SKOV & LAWESSON 2000). In this study, the field data were not used to directly compare the species richness estimators but to validate the assumptions of the simulation as well as the patterns of results from the estimators in the simulation.

The estimators based on the concepts of jackknife and coverage have been studied several times in terms of their performance in estimating population size (e.g. BURNHAM & OVERTON 1979, CHAO ET AL. 1992). However, the simulations used for this task reflected the framework of estimating population sizes in the case of heterogeneous capture probabilities of individuals instead of estimating species richness in the case of different recording probabilities for species within a community.

Simulations have only been used in a few studies to compare the performance of species richness estimators. These simulations were all based on different distributions of species' abundances (compare TOKESHI 1993) the log-normal distribution (BALTANÁS 1992), the negative binomial distribution (WALTHER & MORAND 1998), the gamma distribution (CHAO & BUNGE 2002), and distributions related to stochastic relative abundance models i.e. the broken stick, the random fraction, and random assortment model (BROSE ET AL. 2003, BROSE & MARTINEZ 2004). Most of the estimators compared in these studies are based on incidences of species, whereas the simulations used to compare the estimators are based on the distributions of species' abundances. The step from abundances to distributions of frequencies of species' incidences is affected by factors like effort and the heterogeneity of sampling sites and periods. This study was undertaken to investigate the effect of these factors on the accuracy and reliability of nonparametric incidence-based estimators of species richness. Therefore, a different concept for simulating the species records had to be found.

The simulations generally showed (BALTANÁS 1992, WALTHER & MORAND 1998, CHAO & BUNGE 2002, BROSE ET AL. 2003, BROSE & MARTINEZ 2004) that most species richness estimators tend to underestimate the "true" species richness in the case of effort, which is commonly used. *Jackknife1* is usually negatively biased when the sampling effort is small, except in the case of WALTHER & MORAND (1998), but is robust against spatial heterogeneity caused by differences in the sampling sites and species' mobility (BROSE ET AL. 2003, BROSE & MARTINEZ 2004). *Jackknife2* overestimates when the sampling effort is high (WALTHER & MORAND 1998, BROSE ET AL. 2003). *Moment* is usually a little biased but it is unreliable (BROSE ET AL. 2003, BROSE & MARTINEZ 2004). Therefore, the results for the performance of the estimators of species richness

in the simulation for those estimators which were compared in these papers as well as in this study are generally similar. However, the simulation method used in this study enables the performance of the estimators to be interpreted in terms of factors like sampling effort and sample heterogeneity.

Some of these studies additionally included examples of species richness estimates based on field data (BALTANÁS 1992, WALTHER & MORAND 1998, CHAO & BUNGE 2002). A comparison of the results from the field data with those of the simulations was not possible in these studies because the reasons for the differences in the relative performance of the estimators could not be investigated with the type of simulation used. Thus, the method of simulation used in this study was able to show for the first time that the patterns of results from the species richness estimators are very similar in both simulated and field data in terms of the number of species records and the curve shape of the distribution of species' recording frequencies expressed as CSI (see Chapter 7.4.2).

8.2 Selection of suitable species richness estimators

There have been several attempts to study the performance of species richness estimators in terms of differences in the sampling effort (e.g. WALTHER ET AL. 1995, DOBYNS 1997, BROSE ET AL. 2003) and differences between spatial or temporal samples in the general probability of the species being recorded (BOULINIER ET AL. 1998, BROSE ET AL. 2003, BROSE & MARTINEZ 2004). In these studies it was shown with examples from the field (WALTHER ET AL. 1995, DOBYNS 1997, BOULINIER ET AL. 1998) and simulations (BROSE ET AL. 2003, BROSE & MARTINEZ 2004) that these factors affect the results of species richness estimates. However, the methods of these studies did not enable the complex interactions of these factors to be investigated. Thus, general guidelines as to when to use which estimator of species richness in terms of such factors have not yet been proposed. Moreover, factors which have been found to be important in modeling species abundance patterns like dominance and niche use (TOKESHI 1993) were not investigated in terms of their effect on the performance of species richness estimators.

On the other hand, factors like effort, spatial and temporal heterogeneity, and the characteristics of species and habitats cannot usually be extracted from species records. Moreover, the simulation in this study showed that the effects of the complex interactions of these factors are unpredictable. However, the simulation also showed that two parameters, which can be derived from recording species data, namely the number (of incidences) of species records and the curve shape of the distribution of species' recording frequencies (CSI), reflect these factors. As the number of species records and the CSI are variables of most nonparametric species richness estimators and they can be extracted from species records, they are suitable for selecting the most useful estimator.

Although CHAO ET AL. (1996), NICHOLS ET AL. (1998b), and CHAO ET AL. (2001) proposed the use of the bootstrap method as an alternative nonparametric estimator of the standard error for estimates of species richness and MANLY (1977) suggested using Tukey's jackknife in the closely related field of esti-

imating population parameters, the performance of these methods and the corresponding ones for the species richness estimators have not yet been investigated. Due to their concept, these two estimators seem closely related. However, the performance of the jackknife procedure was strongly dependent on the number of samples. It overestimated the variance in the case of small sample numbers and underestimated it in the case of high ones. Thus, based on the results from the simulation of this study, only the bootstrap procedure can be recommended for estimating the standard error for species richness estimates.

The concept behind the hypotheses of this study (see Chapter 1.3) was to find simple rules to identify those among the studied species richness estimators, which perform best with certain data sets and to confirm the usefulness of nonparametric estimators of the standard error for species richness estimates. Consequently, the results of this study can be formulated in terms of the three hypotheses from the beginning.

The first hypothesis "The distribution of species' recording frequencies is a result of the real abundance of species, the recording effort, and different sources of heterogeneity superimposed on each other" could be validated.

The second hypothesis "The species group, the recording effort, and some of these sources of heterogeneity in samples can be used to indicate which of the species richness estimators will work best" must be rejected. However, the number of species richness and the curve shape index (CSI) are useful to predict this.

The third hypothesis "The bootstrap and jackknife estimators of standard error are useful for species richness estimates" was confirmed for the bootstrap estimator.

8.3 Species richness estimation to correct deficiencies in sampling design?

Some of the studied estimators proved to offer accurate and reliable estimates of species richness, even if the sampling effort was much lower than that of a complete inventory. Thus, if the "deficiency" of a study design is an adequately reduced effort compared to that of a complete inventory, species richness estimation could be a useful tool to repair this. However there are other deficiencies in the sampling design which cannot be repaired by species richness estimation.

Mollusc data from the RIVA project (DEICHNER ET AL. 2003) illustrate that species richness estimation applies to "method communities" and different estimates will result if different methods are applied. Inventories of terrestrial molluscs are usually performed by taking soil samples. In order to get mollusc individuals, the soil samples have to be sieved, either manually or mechanically. The number of recorded individuals, in particular the smaller species, and the number of species was significantly higher when sieving the soil samples mechanically (DEICHNER ET AL. 2003). The difference remained significant when using these samples for estimating species richness. The basic reason for this is that the com-

munity whose species richness is estimated always consists only of species which can be potentially detected using a certain recording method. Thus, the sampled community and consequently its estimated species richness changes, when the sampling method changes. Therefore, the differences between “method communities” are real and there is no reason to expect that a species richness estimator will eliminate these differences.

8.4 Future research

This study showed that two jackknife estimators and two coverage estimators are useful estimators of species richness. The number of species records and the CSI were found to be useful predictors of the best estimator among them for certain data sets. Whereas the jackknife estimators showed their usefulness in estimating species numbers several times (PALMER 1990, PALMER 1991, COLWELL & CODDINGTON 1994, CHAZDON ET AL. 1998, WALTHER & MORAND 1998, BROSE & MARTINEZ 2004), the coverage estimators did this for the first time. Predicting the best species richness estimator for a certain data set using the number of species records and the CSI is a new concept. The bootstrap method was the only one in this study, which was comparable between the species richness estimators and accurately estimated the standard error of species richness estimates. Using the bootstrap method for estimating the standard error of estimates was confirmed by using a simulation for the first time ever. Therefore, an extended study should be conducted to confirm these results.

The scenarios used in the simulation are based on field data from central European floodplains. Other species groups in the tropics for example can consist of a much larger number of species (LONGINO ET AL. 2002, GIMARET-CARPENTIER ET AL. 1998) and may have different structures of dominance. Thus, the results in terms of the precision and reliability of the species richness estimators have to be confirmed by simulation scenarios which model such communities.

This study partly makes up for the lack of investigations comparing the methods of estimating species richness noted by BUNGE & FITZPATRICK (1993). Nevertheless, a future simulation should be able to compare more methods of estimating species richness, which are more or less in use, for example abundance-based estimators of species richness (COLWELL & CODDINGTON 1994, CHAZDON ET AL. 1998, BROSE & MARTINEZ 2004), the Bayesian approach (SOLOW 1994, MIGNOTI & MEEDEEN 1992), and extrapolating and fitting species accumulation curves (SOBERÓN & LLORENTE 1993, COLWELL & CODDINGTON 1994, KEATING & QUINN 1998). Furthermore some new approaches in the rapidly developing field of species richness estimation (PLEDGER 2000, CHAO & BUNGE 2002) should be incorporated in such a comparison.

The quality of biological indication based on presence/absence or the abundance of species depends on recording species, which are important for such indication. This is clearly a function of effort (FOLLNER ET AL. 2002). How can one be sure however of having invested enough time and effort to be able to have recorded most of the important species and, hence, to get a reliable result for an indication?

Species richness estimation can be a tool to ensure the quality of an indication, because it can be assumed, that the difference between the recorded and estimated number of species is a measure of the number of species, which are unseen and would affect the result of the indication. This could become a promising additional application for species richness estimation.

The studied estimators of species richness assume closed species communities. However, some examples with the mobile species group of carabid beetles were most probably not closed in the temporal scale of the sampling (Fig. 58). Since species richness is used as a measure of biodiversity in nature conservation (NICHOLS ET AL. 1998B) the increase or decrease in the number of species in a community in a particular area is a matter of interest. It is usually impractical to get a complete inventory of a species community (BEGON ET AL. 1990). It therefore seems even more impractical to get a time series of such inventories. In such a case an estimation of species richness for open communities is required which corresponds to the estimation of population parameters for open populations. Pollocks robust design (POLLOCK 1982) offers a method for combining the open population approach of Jolly and Seber (JOLLY 1965, SEBER 1965) with methods for estimating the population size of closed populations. NICHOLS ET AL. (1998b) have adapted this robust design to species communities by using a series of species richness estimates based on closed communities for a certain sampling period for studying changes between these sampling periods. In this study, the jackknife estimator (BURNHAM & OVERTON 1978, BURNHAM & OVERTON 1979) was used as a basic estimator of species numbers in the secondary samples of Pollocks robust design to investigate changes in the communities of breeding birds. However, NICHOLS ET AL. (1998b) stated that any other useful estimator of species richness can be used instead. Therefore, all estimators which proved to be highly accurate and reliable in the simulation, can be recommended for this approach.

As species richness is a straightforward measure of biodiversity, it is used in nature conservation as criteria for selecting the most important protected areas. When selecting the most important sites for conservation from a pool of sites to be potentially protected, the highest biodiversity is covered, if the sites are as dissimilar as possible. A useful measure of similarity is a coverage estimator of the number of shared species from two communities (CHAO ET AL. 2000) which is based on the concept of coverage. For this approach as well as for estimating parameters of open communities, a simulation in terms of numbers (of incidences) of species records and the curve shape index of the distribution of species' recording frequencies (CSI) will be a fruitful concept in order to study them.

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10 Summary

The number of species is a straightforward measure of biodiversity in community ecology and conservation. When studying for example the species-area relationship, this measure assumes complete inventories. However, the species lists of a species group from a particular area is usually only a sample of the species community. Therefore, estimating the species richness from samples of species communities has become a recent topic of research. The most progressive and promising methods of species richness estimation appear to be probabilistic nonparametric methods derived from mark-recapture estimators of population size. Species are very different in their probability of being recorded. Choosing estimators which are based on species' recording frequencies and applying the statistical concepts of coverage, of moment estimation, and of jackknife accounts for this.

The object of this study is to identify the factors, which modify the basic probabilities of species being recorded in samples and to model them in order to investigate their effect on estimates of species richness as well as on the associated estimates of standard errors.

This leads to three hypotheses.

- The distribution of species' recording frequencies is a result of the real abundance of species, the recording effort, and different sources of heterogeneity superimposing on each other.
- The species group, the recording effort, and sources of heterogeneity in samples can be used to indicate which of the species richness estimators will work best.
- Bootstrap and Jackknife estimators of standard error are useful for species richness estimates.

In order to be able to compare the accuracy and reliability of species richness estimates, the “true” number of species has to be known. This is the case for simulations, but not usually for field data. Field data are however required to evaluate whether a simulation reflects the ecological reality. In this study, captures from four species groups, i.e. carabid beetles, molluscs, plants, and epigeal spiders provide such field data. The simulation was carried out with scenarios of changing values of the factors known to affect the distribution of species' recording frequencies as well as the numbers of species records and, consequently, the accuracy and reliability of the estimators.

Distributions of species' recording frequencies in field data

Three main factors in the field were found to affect the curve shape of the distribution of species' recording frequencies in a complex way, namely, effort, species' characteristics like the species number and choice of habitats as well as the variability of study sites and study periods. The effects of these factors cannot be separated in the field data. Nevertheless, all curve shapes for the field data clearly differed from the curve shapes for equal recording probabilities. The curve shapes of the distributions of species' recording frequencies covered a range from unimodal with a maximum for small recording frequencies to bimodal with most of the species recorded either only rarely or frequently.

Factors affecting species' recording frequencies in the simulation

Recording frequencies of the species and numbers (of incidences) of species records are important parameters of species richness estimators. Factors, which are known to affect the distribution of species' recording frequencies and the number of species records, have to be studied separately in a simulation in order to be able to subsequently interpret their effect on the performance of species richness estimators. It turned out that the different curve shapes of the distributions of species' recording frequencies can be reflected in one number by the curve shape index (CSI) (1 = only rarely recorded species; 0 = equal numbers of rarely and regularly recorded species with maximums at the extremes; -1 = only regularly recorded species).

The simulation showed that increasing effort, decreasing heterogeneity of the spatial or temporal samples, and increasing width of the habitat gradient used by species groups increased the number of species records and the CSI (more bimodal curves). However, changing the sampling design (e.g. 25 sites with 1 trap each instead of 5 sites with 5 traps each) with constant effort, the number of species records increased whereas the CSI decreased (less bimodal curves). In the simulation, the effect of increasing effort (more species records, increasing CSI) could be countervailed by the effect of increasing heterogeneity (decreasing CSI) or other factors. Thus, even if all values of factors affecting species' recording probabilities are known, as in a simulation, the resulting effect on the distribution of species' recording frequencies and the number of species records is almost unpredictable.

Accuracy and reliability of species richness estimators in the simulation

In terms of the numbers (of incidences) of species records and the CSI, the methods studied for estimating species richness, six coverage estimators, one moment estimator, two jackknife estimators, and one maximum likelihood estimator, achieved the following ratings. The first order jackknife, *Jackknife1*, was usually the most accurate and reliable estimator. Two of the coverage estimators, *Cover1* and *Cover3*, were usually slightly less accurate, however, they performed better in the case of a low CSI (< -0.8) combined with quite low numbers of species records (< 300) and a high CSI (> 0.0) combined with higher numbers of species records (> 300). The second order jackknife, *Jackknife2*, was less accurate and reliable, however, it performed well in the case of a very low number of species records (< 150) and not too high CSI (< -0.1). The other estimators did not reach the accuracy and reliability of these four methods.

None of the factors effort, heterogeneity of samples, characteristics of the species group, or sampling design, or combinations of these are useful criteria to predict the species richness estimator performing best with a particular data set. However, the simulation showed that the number of species records combined with the CSI provides applicable rules. Apart from the fact that generally more species records resulted in a more accurate estimation of species richness, the number of species

records and the CSI do not predict the absolute accuracy of the species richness estimators but the method which is the most accurate and reliable for a given data set.

Estimators of standard error compared by simulation

Generally, the estimators of standard error which were originally provided with the species richness estimators performed satisfactorily. However, standard errors estimated in such a way are not comparable between the estimators of species richness. In order to get a tool to compare standard errors among species richness estimates the bootstrap and the jackknife method was studied. Whereas the bootstrap estimator of standard error worked well, the jackknife method usually clearly overestimated the "true" standard error. Hence, only the bootstrap method can be recommended to replace the corresponding estimators of standard error for the species richness estimators. In detail, the simulation showed some differences between the estimators of species richness.

The bootstrap method of estimating standard errors was always the most accurate and reliable with the coverage estimators and the moment estimator of species richness. With *Jackknife1* the original and the bootstrap method of estimating the standard error were quite similar, however, the original method performed slightly better. With *Jackknife2* the original estimator of standard error was the most accurate and reliable, however, the bootstrap method was also applicable.

Species richness estimators compared to field data

In terms of the number of species records and the CSI, the species richness estimators showed the same patterns of results in the examples with data from the field compared to those in the simulation. Generally, the examples from the field with high numbers (of incidences) of species records and a high CSI for the estimates of species richness were quite similar and the estimated ranges of the standard error were small. In these cases, it can be assumed that the majority of the estimators met the "true" numbers of species well. The simulation showed that all estimators tend to underestimate the species richness when the number of species records and the CSI are low. In such examples from the field *Jackknife1* clearly estimated lower species numbers than the coverage estimators.

General discussion

Most of the previous comparisons of methods for estimating species richness are based on field data. In such studies the "true" number of species is not known and statements about accuracy and reliability of the estimators can only be an educated guess. For some of the comparisons simulations were used which were based on different distributions of species' abundances. However, abundance distributions are the result of the basic catchability of species modified by factors like sampling effort or spatial and temporal heterogeneity of the samples. Studying the effect of these factors on the accuracy and reliability of the estimators therefore involves varying them independently in a simulation.

Therefore, a new concept for simulating the incidences and, consequently, the number of recorded species and the distribution of species' recording frequencies used for species richness estimation is applied in this study.

One purpose of this study was to find an indicator to identify those estimators of species richness for which the most accurate and reliable estimates can be expected with a certain data set. Even if it were possible to derive values for most of the factors like sampling effort as well as spatial and temporal heterogeneity from field data, this would not enable the selection of the best species richness estimator for a definite data set. The guidelines for selecting the most appropriate estimator would be too complicated to be applicable. However, the integrating parameters, number of recorded species and curve shape index (CSI) of the distribution of species' recording frequencies proved to indicate the appropriate estimator.

The general advantage of species richness estimation should be that it requires less sampling effort than a complete inventory of a species community which is often even impossible. As long as the sampling effort is not too drastically reduced, species richness estimation is a useful tool. However, if differences in sampling designs result in a different sampled community, for example by using different trapping methods, species richness estimation cannot counteract this.

The simulation which was used to compare the species richness estimators is based on field data from a central European floodplain. Species communities in the tropics may have many more species and different structures of dominance. Further research is required to confirm that the estimators perform with comparable accuracy and reliability with such data. Moreover, some widely used estimators were not considered in this study.

11 Zusammenfassung

Die Artenzahl ist ein direktes Maß für Biodiversität in der Ökologie von Artengemeinschaften und im Naturschutz. Eine Untersuchung beispielsweise der Artenzahl-Areal-Beziehung verlangt eine vollständige Erfassung der Arten. Die Artenliste einer Artengruppe aus einem Gebiet stellt im Allgemeinen aber nur eine Stichprobe der Artengemeinschaft dar. Deshalb wurde die Artenzahlschätzung auf der Grundlage von Stichproben aus Artengemeinschaften zu einem aktuellen Forschungsthema. Die fortschrittlichsten und vielversprechendsten Methoden der Artenzahlschätzung scheinen probabilistische nonparametrische Methoden zu sein, die von Fang-Wiederfang-Methoden für Populationsgrößenschätzung abgeleitet sind. Arten unterscheiden sich stark in ihrer Nachweiswahrscheinlichkeit. Dies ist berücksichtigt durch die Auswahl von Schätzverfahren, die auf Nachweisfrequenzen und auf den statistischen Ansätzen von „coverage“, statistischem Moment und „jackknife“ beruhen.

Der Gegenstand dieser Untersuchung ist es, Faktoren zu finden, welche die Grundwahrscheinlichkeiten von Arten modifizieren, in Stichproben nachgewiesen zu werden und dies zu modellieren, um ihre Auswirkungen auf Artenzahlschätzungen sowie der Schätzung der zugehörigen Standardfehler zu untersuchen.

Dies führt zu drei Hypothesen:

- Die Frequenzverteilung von Artnachweisen ist das Ergebnis der tatsächlichen Abundanzen der Arten, des Erfassungsaufwandes und verschiedener einander überlagernder Quellen von Heterogenität.
- Die Artengruppe, der Erfassungsaufwand und Quellen von Heterogenität in Stichproben können verwendet werden, um anzuzeigen welcher der Artenzahlschätzer am besten funktionieren wird.
- Bootstrap- und Jackknife- Verfahren können für die Schätzung des Standardfehlers bei Artenzahlschätzungen verwendet werden.

Um die Genauigkeit und Zuverlässigkeit der Artenzahlschätzungen vergleichen zu können, muss die „wahre“ Artenzahl bekannt sein. Dies ist in einer Simulation der Fall, normalerweise jedoch nicht bei Freilanddaten. Freilanddaten sind dennoch notwendig, um beurteilen zu können, ob eine Simulation die ökologische Realität widerspiegelt. In dieser Untersuchung bestehen die Freilanddaten aus Fängen vierer Artengruppen, Laufkäfer, Landschnecken, Pflanzen und bodenbewohnende Spinnen. Die Simulation wurde mit Szenarien mit wechselnden Werten der Faktoren durchgeführt, von denen bekannt war, dass sie die Frequenzverteilungen der Artnachweise sowie die Zahl der Artnachweise und folglich die Genauigkeit und Zuverlässigkeit der Schätzer beeinflussen.

Frequenzverteilungen von Artnachweisen in Freilanddaten

Für drei Hauptfaktoren zeigte sich anhand der Freilanddaten, dass sie die Frequenzverteilung der Artnachweise auf komplexe Weise beeinflussen: Erfassungsaufwand, Variabilität von Untersuchungsflächen

beziehungsweise Untersuchungsperioden und Eigenschaften der Artengruppen, wie Artenzahl und Habitatwahl. Die Einflüsse dieser Faktoren können bei Freilanddaten nicht getrennt werden. Trotzdem unterschieden sich die Kurvenformen in den Freilanddaten deutlich von denen bei gleicher Nachweiswahrscheinlichkeit. Die Kurvenformen der Frequenzverteilungen der Artnachweise deckten einen weiten Bereich ab, von unimodal mit einem Maximum bei den niederen Nachweisfrequenzen bis bimodal, wobei die meisten Arten entweder selten oder regelmäßig nachgewiesen wurden.

Faktoren, die Frequenzverteilungen von Artnachweisen beeinflussen

Frequenzen von Artnachweisen und Anzahlen von Artnachweisen sind wichtige Parameter der Artenzahlschätzer. Faktoren, von denen bekannt ist, dass sie Frequenzverteilungen der Artnachweise und die Anzahl der Artnachweise beeinflussen, müssen einzeln in einer Simulation untersucht werden, um anschließend deren Einfluss auf die Leistung der Artenzahlschätzer beurteilen zu können. Es zeigte sich, dass sich die unterschiedlichen Kurvenformen der Frequenzverteilungen der Artnachweise durch den „curve shape index“ (CSI) in einer Zahl darstellen lassen (1 = nur selten nachgewiesene Arten; 0 = gleich viele seltene und regelmäßige Arten mit Maxima bei den Extremen; -1 = nur regelmäßig nachgewiesene Arten).

Die Simulation zeigte, dass steigender Erfassungsaufwand, sinkende zeitliche und räumliche Heterogenität der Stichproben und steigende Breite des von den Arten genutzten Habitatgradienten die Anzahl der Artnachweise und den CSI steigen ließ (stärker bimodale Kurven). Bei einer Änderung des Probenahmedesigns (z.B. 25 Probeflächen mit 1 Falle anstatt 5 Probeflächen mit 5 Fallen) bei gleichem Erfassungsaufwand stieg die Anzahl der Artnachweise während der CSI fiel (weniger bimodale Kurven). In der Simulation konnte der Einfluss von steigendem Erfassungsaufwand (mehr Artnachweise, steigender CSI) durch den Einfluss steigender Heterogenität der Stichproben (sinkender CSI) oder andere Faktoren ausgeglichen werden. Der resultierende Einfluss auf die Frequenzverteilungen der Artnachweise und die Anzahl der Artnachweise ist deshalb nahezu nicht vorhersagbar, auch wenn, wie in einer Simulation, die Werte aller Faktoren, welche die Nachweiswahrscheinlichkeiten der Arten beeinflussen, bekannt sind.

Genauigkeit und Zuverlässigkeit der Artenzahlschätzer in der Simulation

In Bezug auf die Anzahl der Artnachweise und den CSI erreichten die untersuchten Methoden der Artenzahlschätzung, sechs Coverage-Schätzer, ein Moment-Schätzer, zwei Jackknife-Schätzer und ein Maximum-Likelihood-Schätzer, die folgenden Bewertungen. Der first order jackknife, *Jackknife1*, war gewöhnlich der genaueste und zuverlässigste Schätzer. Zwei der Coverage-Schätzer, *Cover1* und *Cover3*, waren gewöhnlich etwas weniger genau, sie zeigten aber bessere Leistungen bei Kombinationen von niederem CSI (< -0.8) mit ziemlich geringen Anzahlen von Artnachweisen (< 300) und bei Kombinationen von hohem CSI (> 0.0) und hohen Anzahlen von Artnachweisen (> 300). Der second order

jackknife, *Jackknife2*, war weniger genau und zuverlässig, zeigte aber gute Leistungen, wenn die Anzahl der Artnachweise sehr niedrig (< 150) und der CSI nicht zu hoch (< -0.1) war. Die anderen Schätzer erreichten nicht die Genauigkeit und Zuverlässigkeit dieser vier Methoden.

Keiner der Faktoren Erfassungsaufwand, Heterogenität der Stichproben, Eigenschaften der Artengruppe, Probenahmedesign oder Kombinationen von diesen liefern brauchbare Kriterien um den Artenzahlschätzer vorher zu sagen, der mit einem bestimmten Datensatz die beste Leistung zeigt. Die Simulation zeigte jedoch, dass die Anzahl der Artnachweise kombiniert mit dem CSI geeignete Regeln liefert. Abgesehen davon, dass mehr Artnachweise allgemein zu einer genaueren Schätzung der Artenzahl führen, kann mit Hilfe der Anzahl von Artnachweisen und dem CSI nicht die absolute Genauigkeit der Artenzahlschätzer vorhergesagt werden, sondern welche der Methoden die genaueste und zuverlässigste für einen bestimmten Datensatz ist.

Vergleich der Schätzer des Standardfehlers in der Simulation

Die Schätzer des Standardfehlers, die für die Schätzer der Artenzahl ursprünglich vorgesehen waren, arbeiteten im Allgemeinen zufriedenstellend. Standardfehler, die auf solche Weise geschätzt werden, sind jedoch zwischen den Schätzern der Artenzahl nicht vergleichbar. Um ein Werkzeug zu bekommen, mit dem die Standardfehler zwischen den Schätzern der Artenzahl verglichen werden können, wurde die Jackknife- und die Bootstrap-Methode untersucht. Während der Bootstrap-Schätzer für den Standardfehler gut funktionierte, überschätzte die Jackknife-Methode den „wahren“ Standardfehler gewöhnlich deutlich. Deshalb kann nur die Bootstrap-Methode empfohlen werden, die zugehörigen Methoden zur Schätzung des Standardfehlers der Artenzahlschätzer zu ersetzen. Im Detail zeigte die Simulation einige Unterschiede zwischen den Artenzahlschätzern auf.

Die Bootstrap-Methode der Schätzung des Standardfehlers war bei den Coverage-Schätzern und dem Moment-Schätzer der Artenzahl immer die genaueste und zuverlässigste. Bei *Jackknife1* waren die originale und die Bootstrap-Methode der Schätzung des Standardfehlers ziemlich ähnlich, die Originalmethode funktionierte jedoch etwas besser. Bei *Jackknife2* war die Originalmethode der Schätzung des Standardfehlers die genaueste und zuverlässigste, aber auch die Bootstrap-Methode war geeignet.

Vergleich der Artenzahlschätzer mit Freilanddaten

In den Beispielen mit den Freilanddaten zeigten die Artenzahlschätzer in Bezug auf die Anzahl der Artnachweise und den CSI die gleichen Muster der Ergebnisse wie in der Simulation. In Beispielen mit den Freilanddaten mit hohen Anzahlen von Artnachweisen und hohem CSI waren die Schätzungen der Artenzahl im Allgemeinen ziemlich ähnlich und die geschätzten Spannen des Standardfehlers waren klein. Für diese Fälle kann vermutet werden, dass die Mehrheit der Schätzer die „wahre“ Artenzahl gut getroffen hat. Die Simulation zeigte, dass alle Schätzer dazu neigen die „wahre“ Artenzahl zu unterschätzen, wenn die Anzahl der Artnachweise und der CSI niedrig sind. In solchen Beispielen aus den

Freilanddaten schätzte *Jackknife1* deutlich niedrigere Artenzahlen als die Coverage-Schätzer.

Zusammenfassende Diskussion

Die meisten bisherigen Vergleiche von Methoden Artenzahlen zu schätzen beruhen auf Freilanddaten. In solchen Untersuchungen ist die „wahre“ Artenzahl nicht bekannt und Aussagen über die Genauigkeit und Zuverlässigkeit der Schätzverfahren können nur wohl begründete Vermutungen sein. Für einige dieser Vergleiche wurden Simulationen genutzt, die auf unterschiedlichen Verteilungen von Häufigkeiten von Arten beruhen. Häufigkeitsverteilungen sind aber das Ergebnis der Grund-Fangbarkeit der Arten modifiziert durch Faktoren wie Erfassungsaufwand sowie räumliche und zeitliche Heterogenität der Stichproben. Es ist deshalb erforderlich diese Faktoren in einer Simulation unabhängig variieren zu können, um deren Einflüsse auf die Genauigkeit und Zuverlässigkeit der Schätzer untersuchen zu können. Darum wird in dieser Untersuchung ein neuer Ansatz für das Testen von Artenzahlschätzern verwendet, Artnachweise und folglich Anzahlen der Artnachweise und die Frequenzverteilungen der Artnachweise zu simulieren.

Ein Ziel dieser Untersuchung war es, einen Indikator zu finden, mit dem jene Schätzer von Artenzahlen ermittelt werden können, von denen für einen bestimmten Freiland-Datensatz die größte Genauigkeit und Zuverlässigkeit erwartet werden kann. Auch wenn es möglich wäre, aus Freilanddaten für die meisten der Faktoren wie Erfassungsaufwand sowie räumliche und zeitliche Heterogenität in den Stichproben Werte abzuleiten, würde dies nicht erlauben, den besten Artenzahlschätzer für einen bestimmten Datensatz auszuwählen. Die Regeln für die Auswahl des passendsten Schätzers wären zu kompliziert um anwendbar zu sein. Die integrierenden Parameter Anzahl von Artnachweisen und CSI der Frequenzverteilung der Artnachweise zeigten jedoch, dass mit ihrer Hilfe der passende Schätzer ermittelt werden kann.

Die Artenzahlschätzung bietet allgemein den Nutzen, einen geringeren Erfassungsaufwand zu erfordern als eine vollständige Bestandsaufnahme einer Artengemeinschaft, die oft sogar unmöglich ist. Solange der Erfassungsaufwand nicht zu drastisch reduziert wird, ist Artenzahlschätzung ein nützliches Werkzeug. Wenn aber Unterschiede im Stichprobendesign eine andere erfasste Artengemeinschaft ergeben, beispielsweise durch die Verwendung einer anderen Fangmethode, kann die Artenzahlschätzung dies nicht ausgleichen.

Die Simulation, die benutzt wurde, um die Artenzahlschätzer zu vergleichen, beruht auf Freilanddaten aus einer mitteleuropäischen Aue. Artengemeinschaften der Tropen könnten viel mehr Arten und andere Dominanzstrukturen haben. Weitere Untersuchungen sind nötig um zu bestätigen, dass die Schätzer mit solchen Daten mit vergleichbarer Genauigkeit und Zuverlässigkeit funktionieren. Außerdem wurden einige häufig genutzte Schätzer in diese Untersuchung nicht berücksichtigt.

12 Appendix: equations and derivations of the estimators

12.1 Estimators based on the concept of coverage (CoverX)

The basic estimator of population size respectively species richness, *Cover1 – 6*, is:

$$\hat{N} = \frac{\sum_{i=1}^t f_i}{C} + \frac{f_1}{C} * \gamma^2$$

The methods differ in the equations for C , the estimator of the coverage,

$$\hat{C}_1 = 1 - \frac{f_1}{\sum_{i=1}^t if_i} \quad \text{for all coverage- estimators except Cover2 and Cover3 (CHAO ET AL. 1992)}$$

$$\hat{C}_2 = 1 - \frac{f_1 - \frac{2f_2}{t-1}}{\sum_{i=1}^t if_i} \quad \text{for Cover2 (CHAO ET AL. 1992)}$$

$$\hat{C}_3 = 1 - \frac{f_1 - \frac{2f_2}{t-1} + \frac{6f_3}{(t-1)*(t-2)}}{\sum_{i=1}^t if_i} \quad \text{for Cover3 (CHAO ET AL. 1992)}$$

and in the equation for γ^2 , the coefficient of variation, a term which provides corrections for different sources of heterogeneity.

$$\hat{\gamma}_2^2 = \max \left[\frac{\sum_{i=1}^t f_i}{C} * \frac{\sum_{i=1}^t i(i-1)f_i}{2 \sum_{i<j} \sum_{j=1}^t n_i n_j} - 1; 0 \right] \quad \text{for Cover1 to Cover3 (CHAO ET AL. 1992)}$$

$$\hat{\gamma}_1^2 = \max \left[\frac{\sum_{i=1}^t f_i}{C} * \frac{\sum_{i=1}^t i(i-1)f_i}{\sum_{i=1}^t if_i * \left(\sum_{i=1}^t if_i - 1 \right)} - 1; 0 \right] \quad \text{for Cover4 (CHAO & LEE 1992)}$$

$$\hat{\gamma}_2^2 = \max \left[\hat{\gamma}_1^2 * \left(1 + \frac{f_1 * \sum_{i=1}^t i(i-1)f_i}{\sum_{i=1}^t if_i * \left(\sum_{i=1}^t if_i - 1 \right) * \hat{C}} \right); 0 \right] \quad \text{for Cover5 (CHAO & LEE 1992)}$$

$$\hat{y}^2 = \max \left[\frac{\sum_{i=1}^t f_i \sum_{i=1}^t i(i-1)f_i}{C * \left(\sum_{i=1}^t i f_i \right)^2} - 1; 0 \right] \quad \text{for Cover6 (CHAO \& LEE 1993)}$$

The general equation for the variance estimator for *Cover1 - 3* coverage estimators (CHAO ET AL. 1992) is:

$$v \hat{ar}(\hat{N}) \approx \sum_{i=1}^t \sum_{j=1}^t \frac{\partial \hat{N}}{\partial f_i} \frac{\partial \hat{N}}{\partial f_j} cov(f_i, f_j) + \sum_{i=1}^t \sum_{j=1}^t \frac{\partial \hat{N}}{\partial n_i} \frac{\partial \hat{N}}{\partial n_j} cov(n_i, n_j) + 2 * \sum_{i=1}^t \sum_{j=1}^t \frac{\partial \hat{N}}{\partial f_i} \frac{\partial \hat{N}}{\partial n_j} cov(f_i, n_j)$$

with

$$cov(f_i, f_j) = f_i \left(1 - \frac{f_i}{\hat{N}} \right) \quad \text{for } i=j$$

$$cov(f_i, f_j) = \frac{f_i f_j}{\hat{N}} \quad \text{for } i \neq j$$

$$cov(n_i, n_j) = n_i \left(1 - \frac{n_i}{\hat{N}} \right) \quad \text{for } i=j$$

$$cov(n_i, n_j) = \sum_{i,j \in \omega} Z_{\omega} - \frac{n_i n_j}{\hat{N}} \quad \text{for } i \neq j$$

$$cov(f_i, n_j) = \sum_{j \in \omega \# (\omega)=i} \frac{-f_i * n_j}{\hat{N}}$$

The general equation for the variance estimator for *Cover5 - 7* coverage estimators (CHAO & LEE 1992, CHAO & LEE 1993) is:

$$v \hat{ar}(\hat{N}) \approx \sum_{i=1}^t \sum_{j=1}^t \frac{\partial \hat{N}}{\partial f_i} \frac{\partial \hat{N}}{\partial f_j} cov(f_i, f_j) \quad \text{with}$$

$$cov(f_i, f_j) = f_i \left(1 - \frac{f_i}{\hat{N}} \right) \quad \text{for } i=j$$

$$cov(f_i, f_j) = \frac{f_i f_j}{\hat{N}} \quad \text{for } i \neq j$$

Inserting of \hat{y}^2 in the general equation and transforming:

$$\hat{N} = \frac{\sum_{i=1}^t f_i}{C} + \frac{f_1}{C} * \left(\frac{\sum_{i=1}^t f_i}{C} * \frac{\sum_{i=1}^t i(i-1) f_i}{2 \sum_{i<j} \sum_{j=1}^t n_i n_j} - 1 \right)$$

$$\hat{N} = \frac{\sum_{i=1}^t f_i - f_1}{C^2} + \left(\frac{f_1 * \sum_{i=1}^t f_i * \sum_{i=1}^t i(i-1) f_i}{C^2 * 2 \sum_{i<j} \sum_{j=1}^t n_i n_j} \right)$$

$$\hat{N} = \frac{\sum_{i=1}^t f_i - f_1}{C^2} + \frac{1}{2 \sum_{i<j} \sum_{j=1}^t n_i n_j} * \frac{A_1}{C^2}$$

The derivative with respect to f_i of the whole equation:

$$\frac{\partial \hat{N}}{\partial f_i} = - \left(\sum_{i=1}^t f_i - f_1 \right) * C \frac{'}{C^2} + \frac{1}{2 \sum_{i<j} \sum_{j=1}^t n_i n_j} * \left(\frac{A_1' * C^2 - A_1 * 2C * C'}{C^4} \right) \quad \text{for } i=1$$

$$\frac{\partial \hat{N}}{\partial f_i} = \frac{1}{C} - \left(\sum_{i=1}^t f_i - f_1 \right) * C \frac{'}{C^2} + \frac{1}{2 \sum_{i<j} \sum_{j=1}^t n_i n_j} * \left(\frac{A_1' * C^2 - A_1 * 2C * C'}{C^4} \right) \quad \text{for } i>1$$

and with respect to n_i :

$$\frac{\partial \hat{N}}{\partial n_i} = - \frac{A * \sum_{j=i+1}^t n_j}{2 \sum_{i<j} \sum_{j=1}^t n_i n_j * C^2}$$

Inserting \hat{y}^2 in the basic estimator (CHAO & LEE 1992) and transforming to (with $n(1-C) * f_i$):

$$\hat{N} = \frac{\sum_{i=1}^t f_i}{C} + \frac{f_1}{C} * \left(\frac{\sum_{i=1}^t f_i}{C} * \frac{\sum_{i=1}^t i(i-1) f_i}{\sum_{i=1}^t i f_i * \left(\sum_{i=1}^t i f_i - 1 \right)} - 1 \right) * \left(1 + \frac{f_1 * \sum_{i=1}^t i(i-1) f_i}{\sum_{i=1}^t i f_i * \left(\sum_{i=1}^t i f_i - 1 \right) * C} \right)$$

transformed to

$$\hat{N} = \frac{\sum_{i=1}^t f_i - f_1}{C^2} + \left(\frac{f_1 * \sum_{i=1}^t f_i * \sum_{i=1}^t i(i-1)f_i}{C^2 * \sum_{i=1}^t if_i * \left(\sum_{i=1}^t if_i - 1 \right)} \right) - \left(\frac{f_1^2 * \sum_{i=1}^t i(i-1)f_i}{C^2 * \sum_{i=1}^t if_i * \left(\sum_{i=1}^t if_i - 1 \right)} \right) + \left(\frac{f_1^2 * \sum_{i=1}^t f_i * \left(\sum_{i=1}^t i(i-1)f_i \right)^2}{C^3 * \left(\sum_{i=1}^t if_i * \left(\sum_{i=1}^t if_i - 1 \right) \right)^2} \right)$$

$$\text{and } \hat{N} = \frac{\sum_{i=1}^t f_i - f_1}{C^2} + \left(\frac{A_1}{B_1} \right) - \left(\frac{A_2}{B_1} \right) + \left(\frac{A_3}{B_2} \right)$$

The derivative of the whole equation is

$$\frac{\partial \hat{N}}{\partial f_i} = - \left(\sum_{i=1}^t f_i - f_1 \right) * C \frac{'}{C^2} + \left(\frac{A_1' * B_1 + A_1 * B_1'}{B_1^2} \right) - \left(\frac{A_2' * B_1 + A_2 * B_1'}{B_1^2} \right) + \left(\frac{A_3' * B_2 + A_3 * B_2'}{B_2^2} \right) \text{ for } i=1$$

$$\frac{\partial \hat{N}}{\partial f_i} = \frac{1}{C} - \left(\sum_{i=1}^t f_i - f_1 \right) * C \frac{'}{C^2} + \left(\frac{A_1' * B_1 + A_1 * B_1'}{B_1^2} \right) - \left(\frac{A_2' * B_1 + A_2 * B_1'}{B_1^2} \right) + \left(\frac{A_3' * B_2 + A_3 * B_2'}{B_2^2} \right)$$

for $i > 1$

Inserting \hat{y}^2 in the basic estimator (CHAO & LEE 1993) and transforming:

$$\hat{N} = \frac{\sum_{i=1}^t f_i}{C} + \frac{f_1}{C} * \left(\frac{\sum_{i=1}^t f_i}{C} * \frac{\sum_{i=1}^t i(i-1)f_i}{\left(\sum_{i=1}^t if_i - 1 \right)^2} - 1 \right) \equiv$$

$$\hat{N} = \frac{\sum_{i=1}^t f_i - f_1}{C^2} + \left(\frac{f_1 * \sum_{i=1}^t f_i * \sum_{i=1}^t i(i-1)f_i}{C^2 * \left(\sum_{i=1}^t if_i - 1 \right)^2} \right) \equiv$$

$$\hat{N} = \frac{\sum_{i=1}^t f_i - f_1}{C^2} + \left(\frac{A_1}{B_3} \right)$$

The derivative of the whole equation is

$$\frac{\partial \hat{N}}{\partial f_i} = -\left(\sum_{i=1}^t f_i - f_1\right) * C \frac{'}{C^2} + \left(\frac{A_1' * B_3 + A_1 * B_3'}{B_3^2}\right) \quad \text{for } i=1$$

$$\frac{\partial \hat{N}}{\partial f_i} = \frac{1}{C} - \left(\sum_{i=1}^t f_i - f_1\right) * C \frac{'}{C^2} + \left(\frac{A_1' * B_3 + A_1 * B_3'}{B_3^2}\right) \quad \text{for } i > 1$$

The parts of the derivatives

The derivatives for \hat{C} are:

$$\hat{C}_1' = -\frac{\hat{C}}{\sum_{i=1}^t if_i} \quad \text{for } i=1$$

$$\hat{C}_1' = \frac{f_1 * i}{\left(\sum_{i=1}^t if_i\right)^2} \quad \text{for } i > 1$$

$$\hat{C}_2' = -\frac{\hat{C}_2}{\sum_{i=1}^t if_i} \quad \text{for } i=1$$

$$\hat{C}_2' = \frac{2}{t-1} + 2 * \frac{f_1 - \frac{2f_2}{t-1}}{\left(\sum_{i=1}^t if_i\right)} \quad \text{for } i=2$$

$$\hat{C}_2' = i * \frac{f_1 - \frac{2f_2}{t-1}}{\left(\sum_{i=1}^t if_i\right)} \quad \text{for } i > 2$$

$$\hat{C}_3' = -\frac{\hat{C}_3}{\sum_{i=1}^t if_i} \quad \text{for } i=1$$

$$\hat{C}_3' = 2 * \frac{\left(\sum_{i=1}^t if_i + f_1 * (t-1) - 2f_2 + \frac{6f_3}{(t-2)}\right)}{(t-1) * \left(\sum_{i=1}^t if_i\right)^2} \quad \text{for } i=2$$

$$\hat{C}_3' = 3 * \frac{\left(-2 \sum_{i=1}^t i f_i + f_1 * (t-1) * (t-2) - 2 f_2 * (t-2) + 6 f_3 \right)}{(t-1) * (t-2) * \left(\sum_{i=1}^t i f_i \right)^2} \quad \text{for } i=3$$

$$\hat{C}_3' = i * \frac{\left(f_1 * (t-1) * (t-2) - 2 f_2 * (t-2) + 6 f_3 \right)}{(t-1) * (t-2) * \left(\sum_{i=1}^t i f_i \right)^2} \quad \text{for } i > 1$$

The parts in the numerator, A, become:

$$A_1 = f_1 * \sum_{i=1}^t f_i * \sum_{i=1}^t i(i-1) f_i \equiv X * Y$$

$$X = f_1 * \sum_{i=1}^t f_i \quad X' = \sum_{i=1}^t f_i + f_1 \quad \text{for } i=1$$

$$X' = f_1 \quad \text{for } i > 1$$

$$Y = \sum_{i=1}^t i(i-1) f_i \quad Y' = i(i-1)$$

$$A_1' = \left(\sum_{i=1}^t f_i + f_1 \right) * \sum_{i=1}^t i(i-1) f_i + \sum_{i=1}^t f_i * f_1 * i(i-1) \quad \text{for } i=1$$

$$A_1' = f_1 * \sum_{i=1}^t i(i-1) f_i + \sum_{i=1}^t f_i * f_1 * i(i-1) \quad \text{for } i > 1$$

$$A_2 = f_1^2 * \sum_{i=1}^t i(i-1) f_i \equiv X * Y$$

$$X = f_1^2 \quad X' = 2f_1 \quad \text{for } i=1$$

$$(X' = 0) \quad \text{for } i > 1$$

$$Y = \sum_{i=1}^t i(i-1) f_i \quad Y' = i(i-1)$$

$$A_2' = 2f_1 * \sum_{i=1}^t i(i-1) f_i + f_1^2 * i(i-1) \quad \text{for } i=1$$

$$A_2' = f_1^2 * i(i-1) \quad \text{for } i > 1$$

$$A_3 = f_1^2 * \sum_{i=1}^t f_i * \left(\sum_{i=1}^t i(i-1) f_i \right)^2 \equiv X * Y$$

$$X = f_1^2 * \sum_{i=1}^t f_i \qquad X' = 2f_1 * \sum_{i=1}^t f_i + f_1^2 \qquad \text{for } i=1$$

$$X' = f_1^2 \qquad \text{for } i>1$$

$$Y = \left(\sum_{i=1}^t i(i-1) f_i \right)^2 \qquad Y' = 2 \sum_{i=1}^t i(i-1) f_i * i(i-1)$$

$$A_3' = \left(2f_1 * \sum_{i=1}^t f_i + f_1^2 \right) * \left(\sum_{i=1}^t i(i-1) f_i \right)^2 \qquad \text{for } i=1$$

$$A_3' = \left(2f_1 * \sum_{i=1}^t f_i + f_1^2 \right) * \left(\sum_{i=1}^t i(i-1) f_i \right)^2 + f_1^2 * \sum_{i=1}^t f_i * 2 \sum_{i=1}^t i(i-1) f_i * i(i-1) \qquad \text{for } i>1$$

The parts in the denominator, B, become:

$$B_1 = C^2 * \sum_{i=1}^t i f_i * \left(\sum_{i=1}^t i f_i - 1 \right) \equiv X * Y$$

$$X = C^2 \qquad X' = 2C * C' \qquad \text{for } i=1 \text{ \& } i>1$$

$$Y = \sum_{i=1}^t i f_i * \left(\sum_{i=1}^t i f_i - 1 \right) \qquad Y' = 2 \sum_{i=1}^t i f_i - 1 \qquad \text{for } i=1$$

$$Y' = 2 \sum_{i=1}^t i f_i * i - i \qquad \text{for } i>1$$

$$B_1' = 2C * C' * \sum_{i=1}^t i f_i * \left(\sum_{i=1}^t i f_i - 1 \right) + C^2 * \left(2 \sum_{i=1}^t i f_i * i - i \right) \qquad \text{for } i=1 \text{ \& } i>1$$

$$B_2 = C^3 * \left(\sum_{i=1}^t i f_i * \left(\sum_{i=1}^t i f_i - 1 \right) \right)^2 \equiv X * Y$$

$$X = C^3 \qquad X' = 3C^2 * C' \qquad \text{for } i=1 \text{ \& } i>1$$

$$Y = \left(\sum_{i=1}^t i f_i * \left(\sum_{i=1}^t i f_i - 1 \right) \right)^2 \qquad Y' = 2 \sum_{i=1}^t i f_i * \left(\sum_{i=1}^t i f_i - 1 \right) * \left(2 \sum_{i=1}^t i f_i - 1 \right) \qquad \text{for } i=1$$

$$Y' = 2 \sum_{i=1}^t i f_i * \left(\sum_{i=1}^t i f_i - 1 \right) * \left(2 \sum_{i=1}^t i f_i * i - i \right) \qquad \text{for } i>1$$

$$B_2' = 3C^2 * C' * \left(\sum_{i=1}^t if_i * \left(\sum_{i=1}^t if_i - 1 \right) \right)^2 + C^3 * 2 \sum_{i=1}^t if_i * \left(\sum_{i=1}^t if_i - 1 \right) * \left(2 \sum_{i=1}^t if_i * i - i \right)$$

for $i=1$ & $i>1$

$$B_3 = C^2 * \left(\sum_{i=1}^t if_i \right)^2 \equiv X * Y$$

$$X = C^2 \qquad X' = 2C * C' \qquad \text{for } i=1 \text{ \& } i>1$$

$$Y = \left(\sum_{i=1}^t if_i \right)^2 \qquad Y' = 2 \sum_{i=1}^t if_i * i \qquad \text{for } i=1 \text{ \& } i>1$$

$$B_1' = 2C * C' * \left(\sum_{i=1}^t if_i \right)^2 + C^2 * 2 \sum_{i=1}^t if_i * i \qquad \text{for } i=1 \text{ \& } i>1$$

12.2 Moment estimator (Moment)

of (CHAO 1984, CHAO 1987, CHAO 1988) is:

$$\hat{N} = \sum_{i=1}^t f_i + \frac{f_1^2}{2f_2}$$

$$v \hat{a}r(\hat{N}) = f_2 * \left(\frac{(f_1/f_2)^4}{4} + (f_1/f_2)^3 + \frac{(f_1/f_2)^2}{2} \right)$$

12.3 Jackknife estimators (JackknifeX)

of (BURNHAM & OVERTON 1978, BURNHAM & OVERTON 1979) is:

first order jackknife (*Jackknife1*)

$$\hat{N}_{J1} = \sum_{i=1}^t f_i + \left(\frac{t-1}{t} \right) * f_1$$

$$v \hat{a}r(\hat{N}_{J1}) = \left(\frac{t-1}{t} + 1 \right)^2 * f_1 + \sum_{i=1}^t f_i - f_1 - \hat{N}_{J1}$$

an alternative estimator of the variance of HELTSHE & FORRESTER 1983

$$v \hat{a}r(\hat{N}_{J1}) = \left(\frac{t-1}{t} \right) * \left(\sum_{i=1}^D i^2 n_i - \frac{f_1^2}{\sum_{i=1}^t if_i} \right) \text{ with } D = \sum_{i=1}^t f_i \text{ and } n_i \text{ the number of capture sessions, dur-}$$

ing which exactly i species were recorded solely.

second order jackknife (*Jackknife2*)

$$\hat{N}_{J2} = \sum_{i=1}^t f_i + \left(\frac{2t-3}{t} + 1 \right) * f_1 - \left(\frac{(t-2)^2}{t*(t-1)} \right) * f_2$$

$$v \hat{ar}(\hat{N}_{J2}) = \left(\frac{2t-3}{t} + 1 \right)^2 * f_1 + \sum_{i=1}^t f_i - f_1 - f_2 - \hat{N}_{J2}$$

Originating in the results of the exemplary data set, in (BURNHAM & OVERTON 1978) the above equation has been used, however, following the instructions another formula could be correct.

$$v \hat{ar}(\hat{N}_{J2}) = \left(\frac{2t-3}{t} + 1 \right)^2 * f_1 + \left(\frac{(t-2)^2}{t*(t-1)} + 1 \right)^2 * f_2 + \sum_{i=1}^t f_i - f_1 - f_2 - \hat{N}_{J2}$$

12.4 Maximum Likelihood estimator (*MaxLike*)

as shown in (OTIS ET AL. 1978) is:

$$\hat{N} = N \text{ with } \max[\ln L]$$

$$\ln L(N, p|X) = \ln \left(N \frac{!}{\left(N - \sum_{i=1}^t f_i \right)!} \right) + \sum_{i=1}^t i f_i * \ln \left(\frac{\sum_{i=1}^t i f_i}{t * N} \right) + \left(t * N - \sum_{i=1}^t i f_i \right) * \ln \left(1 - \frac{\sum_{i=1}^t i f_i}{t * N} \right)$$

$$v \hat{ar}(\hat{N}) = \hat{N}_0 * \left[\left(1 - \frac{\sum_{i=1}^t i f_i}{t * N} \right)^{-t} - t * \left(1 - \frac{\sum_{i=1}^t i f_i}{t * N} \right)^{-1} + t - 1 \right]^{-1}$$

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