



Frequent and occasional species and the shape of relative-abundance distributions

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ABSTRACT

Recently, three different models have been proposed to explain the distribution of abundances in natural communities: the self-similarity model; the zero-sum ecological drift model; and the occasional–frequent species model of Magurran and Henderson. Here we study patterns of relative abundance in a large community of forest Hymenoptera and show that it is indeed possible to divide the community into a group of frequent species and a group of occasional species. In accordance with the third model, frequent species followed a lognormal distribution. Relative abundances of the occasional species could be described by the self-similarity model, but did not follow a log-series as proposed by the occasional–frequent model. The zero-sum ecological drift model makes no explicit predictions about frequent and occasional species but the abundance distributions of the hymenopteran species did not show the excess of rare species predicted by this model. Separate fits of this model to the frequent and to the occasional species were worse than the respective fits of the lognormal and the self-similarity model.

Keywords

Ecological drift, hymenoptera, lognormal, log-series, parasitoids, relative-abundance distribution, self-similarity, zero-sum multinomial.

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INTRODUCTION

Explaining differences in abundances of species is central to community ecology. The observation that plots of abundance vs. species rank orders (relative-abundance distributions, RADs) often have simple geometric shapes has intrigued ecologists and resulted in a large number of different theoretical models (Tokeshi, 1993, 1999 and Hubbell, 2001). Classical models tried to explain the shape of RADs (in particular the lognormal) either on sample theoretical bases (Fisher *et al.*, 1943; Preston, 1962; May, 1975) or on niche division processes (Sugihara, 1980; Tokeshi, 1993). Recently, the frequently observed excess of rare species (manifest in the left skewed shapes of RADs in log-abundance–species-number plots) captured the attention of ecologists (Nee *et al.*, 1991; Hubbell, 2001).

Two recent neutral theories try to explain the observed RAD shapes either from zero-sum ecological drift (Solé *et al.*, 2000; Bell, 2001; Hubbell, 2001) or from self-similar patterns of species accumulation (Frontier, 1985; Solé & Alonso, 1998; Moulliot *et al.*, 2000). The ecological drift model predicts RADs whose shape is given by a zero-sum multinomial distribution, which can be log-series or log-normal like (Hubbell, 2001). The model predicts that most communities should have left skewed RADs in log-abundance–species-number plots (ASPs) and pronounced

lower downward curvatures of rank–log-abundance plots (RAPs) made up by the relatively rare species (Fig. 1). The self-similarity model instead generates RADs that follow power function RAPs. Both models assume that all species of a community contribute to a common relative-abundance distribution.

Magurran & Henderson (2003) instead argued that communities can be divided into a group of frequent species, which are permanent members of a focal community, and a group of occasional species, which enter the community from time to time. The latter group contains therefore species with relatively high local extinction and immigration rates. For frequent species Magurran & Henderson (2003) predict a lognormal type RAD and for occasional species a log-series distribution. The latter distribution follows if simple Poisson processes generate temporal persistence patterns (Fisher *et al.*, 1943).

However, critical tests of all three models are still scarce (Fargione *et al.*, 2003; Hubbell, 2003; McGill, 2003; Ricklefs, 2003; Volkov *et al.*, 2003). Here, we present data about abundances in a large local community of forest Hymenoptera. We will show that the more frequent species of this community indeed follow a lognormal distribution as predicted by Magurran & Henderson (2003). Abundance distributions of the more infrequent species instead can be described by the self-similarity model.

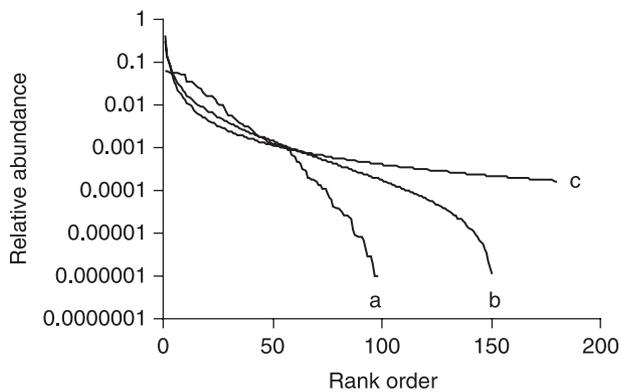


Figure 1 Typical relative abundance–species–rank-order plots of (a) an assemblage generated by ecological drift ($\theta = 50$) (b) a lognormal, and (c) an assemblage generated by the self-similarity model. Note the upper and lower curvature in all these models.

MATERIAL AND METHODS

We use data about local densities and species numbers of Hymenoptera obtained in a long-term quantitative sampling program for estimating arthropod densities and biomasses in a beech forest (Melico-Fagetum; Subass. *Lathyrus vernus*) on limestone near Göttingen (northern FRG) (Schaefer, 1996, 1999). Between 1980 and 1987 a total of 144 m² of forest floor was quantitatively sampled with one (1980), 24 (1981, 1982), 16 (1983), 20 (1984, 1985), and 24 (1986, 1987) emergence traps that covered 0.25 m² (1984, 1985) and 1 m² of forest floor each. A detailed description of the sampling program as well as annual abundance and biomass data for each species is contained in Ulrich (1998, 2001a). In total 43695 individuals out of 720 hymenopteran species were caught.

For comparison all data refer to emergence densities computed from the total number of individuals per species and year divided through the total area the traps covered. Mean densities of frequent and occasional species refer always to arithmetic means during the whole study period; hence zero counts are included. We excluded in all cases the first sample obtained after the placement of the traps. These samples might contain individuals which were enclosed under the trap during placement but did not emerge. Including these individuals would give too high density estimates for species associated with the herb layer and the soil. This procedure led also to the elimination of 70 species which were found exclusively in such samples. These are species found exclusively in only one of the sampling years. For comparison we included these 70 species in the group of occasional species found in only one year and performed the same analyses as below. The results were virtually identical to those shown below.

We also excluded all nest building aculeate species because they were not sampled quantitatively (in total 22 species out of the families Vespidae, Formicidae, Sphecidae, Megachilidae, and Apidae). The following analysis is therefore based on catches of 33,761 individuals out of 628 species.

Reliable comparisons of deterministic models with stochastic ones, such as the ecological drift model, have not only compared

means but also variances (Tokeshi, 1990, 1993). These have to be estimated from sample theoretical models. Here we use a normally distributed random number at a logarithmic scale to fit the lognormal to rank-order–log-abundance plots. The distribution has a single shape generating parameter, the variance. By adjusting this variance the distribution can be fitted to a given data set. Such a fitting is done by a RAD fitting package (Ulrich, 2002) that is based on a least square statistic for finding the best solution. We used the modified random assortment algorithm of Tokeshi (1990) to approximate the log-series (Ulrich, 2002). This sequential breakage model is defined by

$$A_i = A_{\min(i-1)} \text{ran}^z \quad (1)$$

where A_i is the abundance of species i ; $A_{\min(i-1)}$, the smaller breakage product of species $i-1$; ran , a linear random number between 0 and 1; and z , a shape generating parameter (Ulrich, 2002). We approximated the self-similarity model (the power function) by a stochastic version (Mouillot *et al.*, 2000) defined by

$$A_i = (\text{ran} + X)^{-z} \quad (2)$$

where X and z are two shape generating parameters (Ulrich, 2002).

Lastly, we used the species generator method described in Hubbell (2001; pp 289 ff) and implemented in RAD (Ulrich, 2002) to fit the ecological drift model under the point mutation speciation mode to our data set. The model is defined by two parameters, the fundamental biodiversity number θ and a parameter that describes dispersal limitation.

Fits by these four models were compared with the 95% confidence limit method of Tokeshi (1990). The latter counts the number of data points that range outside the 95% confidence limits of the model to be fitted. We determined the respective confidence limits from 100 randomizations of each model.

For fitting log-series and lognormal distributions to species-number–octave plots conventional CHI² and Kolmogorov–Smirnov tests of STATISTICA 5 (Statsoft, 1997) were used according to Wilson (1991).

One might criticize that the above described methods of defining variances for deterministic models are too artificial. However, previous work on RAD models often failed to appreciate the importance of sample variance (Tokeshi, 1990, 1993; Bersier & Sugihara, 1997) with the result that classical tests of fit like the CHI² or the Kolmogorov–Smirnov test gave false impressions in being too conservative. This bears the danger of making type II errors while rejecting a correct model. The use of stochastic algorithms tries to avoid this type of error.

RESULTS

The RAD of the forest Hymenoptera, when taking mean densities of all species caught, has a hollow shape that is typical for samples from species rich arthropod assemblages (Fig. 2) (Stork, 1987; Morse *et al.*, 1988; McGill & Collins, 2003). None of the models tested here, lognormal, log-series, self-similarity and

Table 1 Fractions of species ranging outside the 95% confidence limits in log-abundance–species-rank-order plots of the four models tested. The lognormal model gives the best fit for frequent species, the self-similarity model for occasional species

Model	Whole community	Years found					
		at least		at least		at most	
		8	7	6	1	2	3
Lognormal	0.49	0	0	0	0.92	0.89	0.81
Log-series	0.78	0.05	0.11	0.31	0.85	0.84	0.77
Self-similarity	0.81	0.01	0.03	0.02	0.01	0	0.02
Ecological drift	0.70	0.05	0.09	0.37	0.010	0.65	0.61

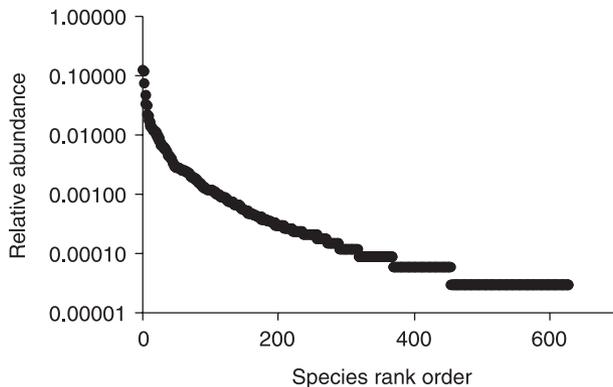


Figure 2 Relative-abundance distribution of 628 beech forest Hymenoptera.

ecological drift model, fits well to this RAD. For every model more than 65% of all data points ranged outside the 95% confidence intervals (Table 1).

Frequent species closely followed lognormal RADs. All data points in Fig. 3 a to c range inside the 95% confidence interval of the stochastic lognormal model used here. A CHI^2 test did not point to significant deviations of the data points from model expectation (CHI^2 of no deviation: $P > 0.1$). Species-number–octave plots did not deviate from normality (Fig. 4a; CHI^2 : $P > 0.1$). In this group of frequent species no excess of rare species occurred that would cause asymmetrical shapes of both types of plots. The log-series (Fig. 4a) and the ecological drift model (Figs 4a and 5a), on the other hand, did not fit well to the data (Table 1).

RADs of the occasional species (those found in at most three study years) did not follow log-series (Table 1, Figs 3d–f, 4b and 5b). Instead, they are closely fitted by power functions as predicted by the self-similarity model. The ecological drift model makes no explicit predictions about frequent and occasional species. It predicts instead, at least for species rich assemblages, a marked lower curvature in rank–log-abundance plots and a high number of very rare species (Hubbell, 2001; McGill, 2003). The Hymenoptera of this study do not show such a pattern (Fig. 2a). Fits of the model were in both cases worse than those by the self-similarity model (Figs 4b and 5).

DISCUSSION

The present paper relies on a grouping of forest Hymenoptera into frequent and occasional species. Of course, the grouping criterion used here (at most three and more than six years found) is somewhat artificial. There is surely a continuum between frequent and occasional species. However, the above results cannot only be explained from sample artifacts. It would be easy to model the expected RADs of frequent and occasional species if they were only the result of a passive sampling process. For this task we took eight random samples from the total of 33,761 individuals and 628 species that contained the real yearly numbers of individuals sampled (Fig. 6). The frequent species (present in more than six samples) of such random samples closely follow the upper part of the RAD of all hymenopteran species (Fig. 1). Their RAD deviates from a lognormal while lacking the lower curvature (Fig. 6). The occasional species (present in at most three samples) instead follow a log-series RAD as expected from a Poisson random process (Fisher *et al.*, 1943). All of the data points in Fig. 6 ranged inside the 95% confidence limit of the log-series model used here (1). Instead 27% of the data points ranged outside the 95% confidence limit of the power function model (data not shown). This pattern is very similar to the one found by Magurran & Henderson (2003) in their study on estuarine fish communities but clearly deviates from the power function distribution shown in Fig. 2.

Our grouping into frequent and occasional species has a long tradition in ecology and appears to be similar to the distinction between core and satellite species of Hanski (1982). The classical r - K model of MacArthur & Wilson (1967) predicts also species which are permanent members of a given habitat, and a group of potentially colonizing species which enter the habitat from time to time (Pianka, 1970). It would be interesting to see whether core and satellite species or r and K strategists follow different RADs as found in the present study.

The frequent hymenopteran species were lognormal type distributed. However, the distribution clearly deviated from the canonical hypothesis in being more even than predicted by Preston (1962) and May (1975). The ecological drift model predicts lognormal type RADs but does not distinguish between frequent and occasional species and is therefore silent about

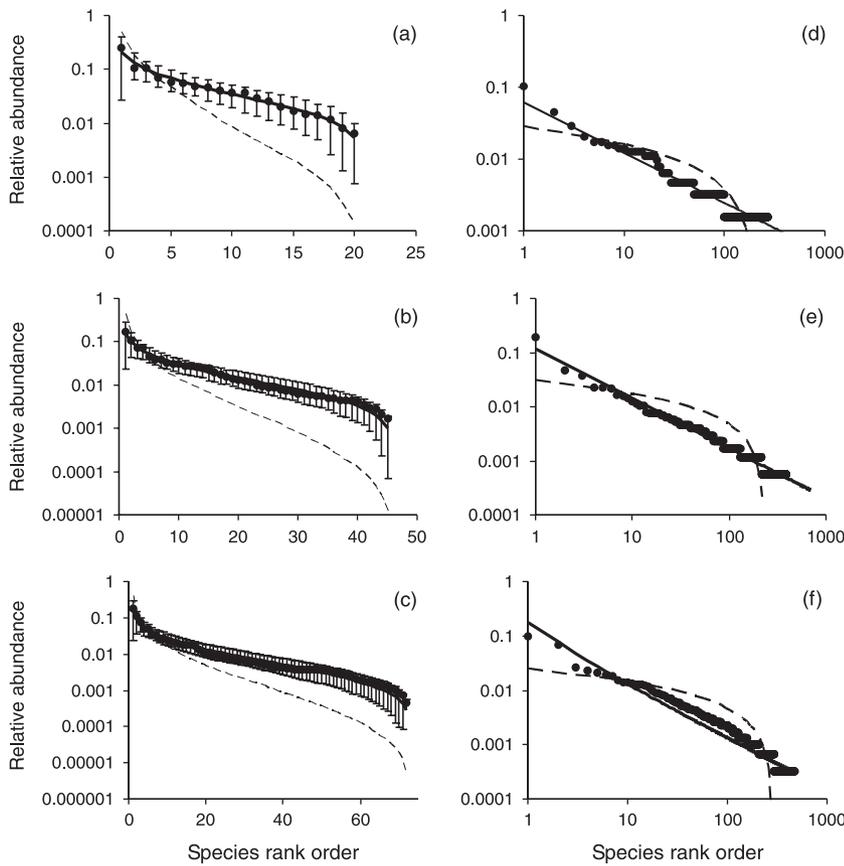


Figure 3 (a–c) Rank-order–log-abundance plots of frequent species (a) species found in all study years; (b) species found in at least seven years; (c) species found in at least six years) follow lognormal type distributions. Regression lines give fits of the stochastic approximation to the lognormal (Ulrich, 2002). None of the data points ranges outside the 95% confidence limit of the model (the error bars). The broken lines give the expectations of a canonical lognormal. (d–f) RADs of infrequent species; (d) species found in only one study year; (e) species found in at most two years; and (f) species found in at most three years) are much better fitted by power functions (full lines; R^2 in all cases > 0.94) than by log-series (broken lines; R^2 in all cases < 0.55). With respect to readability error bars in d, e, and f were omitted. In all three plots more than 50% of the data points ranged outside the 95% confidence limit of the log-series model. The respective values for the power function were 11% (d), 0% (e), and 0% (f).

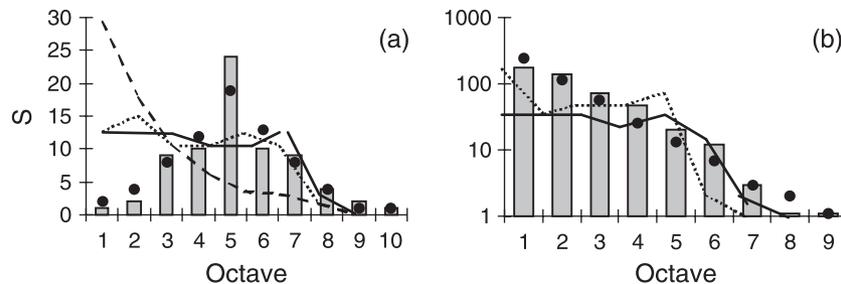


Figure 4 Species number (S) — octave plots of the species found in at least 6 study years (a) and in at most 3 study years (b). Dots in a give the expectation of a lognormal distribution and in b the expected species numbers of the self similarity model. Full lines are in both figures the expected species numbers of a log-series. Dotted lines are respective fits by the ecological drift model (means of 100 replicates, without dispersion limit; a: fitted $\theta = 19.5$, b: fitted $\theta = 130$). The broken line in a gives the fit of the self-similarity model. The distributions in a and b do not significantly deviate from the dotted models ($\text{CHI}^2: P > 0.1$) but deviate significantly from the expectations of a log-series and from the ecological drift model ($\text{CHI}^2: P < 0.01$).

frequency distributions of both groups. It remains to be seen whether the model is able to predict the patterns observed. This might be another way to test this model.

The self-similarity model does not predict lognormal RAD patterns in frequent species but seems to be appropriate to explain abundance patterns in infrequent species. To explain the observed abundance patterns we have to assume that temporal patterns of variability are also self-similar. This seems not improbable in the light of recent studies, where frequency distributions of rarity (Ferriere & Cazelles, 1999) or temporal

variability (Rhodes & Anderson, 1996; Halloy, 1998) were found to be self-similar.

The RADs of the more infrequent species did not follow log-series as found by Magurran & Henderson (2003). They assumed that simple Poisson processes govern local species turnover rates and abundances. In this case the variance : mean ratio should be approximately 1 ($\sigma^2 \propto \mu$). Such a Poisson process translates into a log-series RAD as had already been shown by Fisher *et al.* (1943). However, patterns of temporal variability follow, at least in insects, more often Taylor's power law (a pattern of proportional

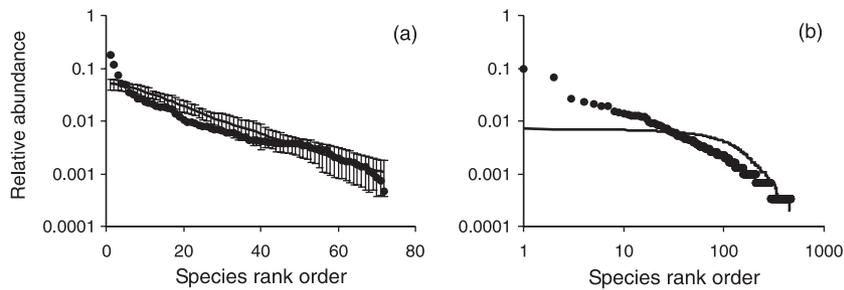


Figure 5 Rank-order-log-abundance plots of the species found in at least 6 study years (a) and in at most 3 study years (b). Full lines and error bars give fits by the ecological drift model and 95% confidence limits (means of 100 replicates, a: fitted $\theta = 19.5$, b: fitted $\theta = 170$). With respect to readability, error bars in b were omitted. In a 32% of all data points and in b 85% of all data points range outside the confidence limits of the model. In a and b χ^2 and Kolmogorov–Smirnov tests did not point to acceptable fits (in a and b: $P > 0.1$).

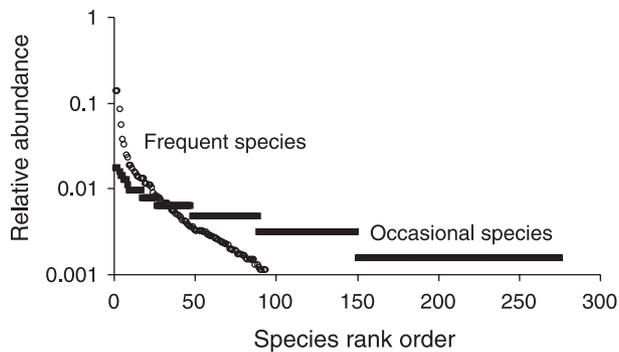


Figure 6 Simulating RADs of frequent and occasional species. Eight random samples having as many individuals as found in each of the eight study years in the beech forest were taken from the total hymenopteran community used in this study (33761 individuals and 628 species). The resulting RAD of the species found in at least six samples (frequent species) are not lognormally distributed. The RAD of the species found in at most three samples (occasional species) is a typical log-series.

rescaling) with $\sigma^2 \propto \mu^z$ and z being around 2 (Taylor, 1961; Taylor *et al.*, 1980; Soberon & Loevinsohn, 1987; Leps, 1993; Kilpatrick & Ives, 2003). Indeed, Magurran & Henderson did not explicitly test a power function model against their data. How Taylor's power law translates into relative-abundance distributions in infrequent species has, as far as we know, not been studied. Ulrich (2001a) showed already that the Hymenoptera neatly follow Taylor's power law ($z = 2.17$; $R^2 = 0.92$). That occasional species can be described by a power function RAD points to the possibility that Taylor's power law (a power function) translates also into a power function RAD.

Symmetric lognormal type distributions appear when many independent factors act together in a multiplicative way to structure closed communities (May, 1975; Sugihara, 1980; Nee *et al.*, 1991). If instead stochastic dispersal were the dominating structuring force, abundance distributions should significantly deviate from lognormality. We found such a deviation in the occasional species. From this we conclude that abundance patterns of these species might be shaped by dispersal. However, our results indicate that dispersal is not a simple

Poisson process as had been assumed by Magurran & Henderson (2003).

Closely related to the question about relative abundances is the question why most species in animal communities are rare (Gaston, 1994; Rosenzweig & Lomolino, 1997). All four models considered here try to answer this question on the basis of stochastic processes. The ecological drift model predicts pronounced differences in densities between the most and least abundant species and an excess of very rare species (Fig. 1) (Hubbell, 2001). The self-similarity model instead gives for reasonable parameter values much lesser absolute differences in abundance. Lognormal and log-series are intermediate in this respect. We did not find an excess of very rare species. This might, of course, be a sample effect. No sampling protocol is able to screen the whole forest to find even the rarest species. However, the worse fit of the ecological drift model and the lack of any lower curvature in the log-abundance-rank-order plots of infrequent species (Figs 3 and 5) do not point to the presence of many undetected very rare species. It seems instead that the absolute differences in abundance between the most and the least abundant species are much less than predicted by most theories. Frequent species appeared to be much more evenly distributed than predicted by the classical canonical lognormal, which was long held to be the one expected in an assemblage under the influence of many stochastic environmental forces (May, 1975; Sugihara, 1980).

We can turn the whole argument on the head and ask how large the absolute differences in abundance have to be so that a lognormal would fit to the data. The most parsimonious estimate is about 10^8 and stems from Fig. 1(a), where we assume a symmetric shape of the RAD. Given that the most abundant hymenopteran species of this study had mean densities of about 10 individuals per m^2 (Ulrich, 2001a) the least abundant species should then have mean densities of 1 individual per 10 km^2 or even less. We are not aware of any arthropod study that reports such differences in local abundances from a single taxon (except for outbreak species).

Our results also imply an answer to the question with what kind of community theories and models of relative abundance should deal. They should incorporate dispersal patterns and differentiate between frequent and occasional species. For frequent species models that focus on niche division and species

interactions might be appropriate (Fesl, 2002). Abundances of occasional species instead should be modelled from stochastic dispersal patterns. These models should also deal with patterns of temporal variability (Ulrich, 2001b).

Further studies have to test whether the ecological drift approach is able to generate a temporal frequent-species–occasional-species pattern of species occurrences or mean densities and leads to log-series or power function RADs of locally infrequent species. Surely, much more data from long-term quantitative studies are necessary to infer what factors govern temporal occurrence patterns and abundances in animal and plant assemblages.

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