Modelling species richness and diversity in grassland communities of the Central Caucasus

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In this study I used small squares (4 cm × 4 cm) as a sampling technique within plots (128 cm × 128 cm) of different elevation, aspect and slope angle in grassland communities (20 plots examined). Then I used a rectangular hyperbole equation (the Michaelis-Menten model) to describe species richness and the Inverse of Simpson Concentration (ISC) as functions of sample size. I checked robustness and precision of the model both by interpolation and extrapolation. Interpolation was similarly good in both cases, while extrapolation produced reliable predictions of ISC but underestimated species richness. Dominance analysis indicated that the underestimation of richness depends on the proportion of bottom species, and that the predicted values of richness roughly coincide with the numbers of dominant species found in plots. Therefore, the model may be used to assess number of dominant species when precision is less important than saving time during a survey. However, the rectangular hyperbole equation appears to be precise and robust in the prediction of ISC, at least in grassland communities. This property may also be employed for extrapolation of diversity indices with a limited sampling effort.

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The equation of the rectangular hyperbole, also known as the Michaelis-Menten model, is a popular means of estimating species richness based on species accumulation curves. However, recent empirical and theoretical tests demonstrate that this model is neither accurate nor robust when applied to certain community types (Palmer 1990, 1991; for a review see Keating 1998). Richness is an index of diversity that ignores species frequencies, while the Michaelis-Menten model implicitly assumes an even frequency distribution of species in a community. Since species accumulation curves have different shapes in communities of different structure, the Michaelis-Menten model may not fit cases of highly uneven frequency distribution of species (Crawley 1997, Keating 1998). Conversely, other commonly used indices of species diversity such as the Shannon index or the Inverse of Simpson Concentration are based on species frequencies. These indices are functions of sample size as well, and may have shapes similar to species accumulation curves (Lande 1996, Smith and Wilson 1996).

Although considerable attention has been focused on using the Michaelis-Menten model to estimate species richness, there have been few (if any) attempts to extrapolate frequency-based diversity indices. Another point deserving consideration is that since community structure influences the species accumulation curve, deviations of the latter from the Michaelis-Menten model may be employed to analyse the former. Accordingly, the purpose of my study was twofold: (1) to find whether the Michaelis-Menten model performs well in relation to frequency-based diversity indices and (2) to explore whether this model helps to analyse plant community structure.

Study area and methods

I conducted my study in sub-alpine and alpine pastures of the Kazbegi District in the Central Caucasus (Georgia, 42°48′N, 44°39′E), on grassland communities of alpine and sub-alpine pastures on the southwestern slope of Mt. Kazbegi (Kazbek, 5033 m a.s.l.).

I collected data from 128 cm × 128 cm plots with a grid of 1024 small 4 cm × 4 cm squares. I randomly sampled 100 squares per plot. Twenty plots were established, I chose the particular locations of plots subjectively to sample homogeneous areas. The plots were of different aspect and slope, altitude 2300 to 2850 m a.s.l. (Table 1). For each plot, I calculated two values: (a) S_{100}, or the total number of species found in 100 squares per plot and (b) $1/\lambda_{100}$, or the Inverse of Simpson's Concentration (hereafter ISC) from the same 100 squares. λ was calculated as

$$\lambda = \sum p_i^2,$$

where p_i is relative frequency of species among squares in a plot.

I examined frequency distributions by means of dominance-diversity curves (Kent and Coker 1996) and dominance analysis (Ohsawa 1984). The latter distinguishes top and bottom species by their frequencies. The actual frequencies are compared to a model with an even frequency distribution of variable species number (1 to S_{100} in my case). Deviation d from an even frequency distribution at different number of species is calculated by the equation:

$$d = 1/S_{100}\left\{ \sum (x_i - x')^2 + \sum (x_j^2) \right\},$$

$$i = 1, \ldots, T, \quad j = 1, \ldots, U; \quad i + j = T + U = S_{100};$$

where x_i is the frequency of the top species (T), x' is the theoretical frequency assuming an even distribution of the given number of species, and x_j is the frequency of the bottom species (U). S_{100} is the total number of species found in 100 squares. T at minimum d is the number of top species.

I adopted the number of sampled squares as units of sampling effort. With the given sampling effort, I fixed both the number of species and the calculated values of ISC to build their respective accumulation curves. I calculated average curves based on 10 randomised orders of counting squares. Within the range of sampling effort of 1 to 10 squares I fitted the Michaelis-Menten model using rectangular hyperbolic equations. In cases of species richness and ISC accumulation, respectively, the equations are:

$$S(n) = S \times n/(B_s + n)$$

and

$$1/\lambda(n) = 1/\lambda \times n/(B_{1/\lambda} + n),$$

where $S(n)$ is the number of species observed after n units of sampling, S is the total richness of the plot and B_S is the sampling effort required to detect exactly 50% of S; $1/\lambda(n)$ is the value of $1/\lambda$ observed after n units of sampling, $1/\lambda$ is the total diversity in plot and $B_{1/\lambda}$ is the sampling effort required to detect exactly 50% of $1/\lambda$.

A popular method of fitting the Michaelis-Menten model, both in enzyme kinetics and species richness estimations, is the method of Lineweaver-Burke. However, this is the least accurate of the available techniques, whereas the method of Eadie-Hofstee is more flawless (Cornish-Bowden 1995). I chose the method of Eadie-Hofstee to analyse the average curves, as it is

Table 1. Characterisation ($EE_{1/\lambda}$) of studied plots.

Plot	Altitude (m a.s.l.)	Aspect	Slope (°)	Cover (%)
A	2270	S	20	93
B	2290	SSE	10	90
C	2300	ESE	5	90
D	2330	NNE	15	85
E	2320	NNE	25	90
F	2410	S	20	95
G	2430	SSE	15	95
H	2460	0	0	90
I	2450	N	10	90
J	2420	N	15	95
K	2650	SSE	25	90
L	2670	SSE	5	95
M	2690	0	0	80
N	2680	NNW	20	90
O	2680	NNW	30	90
P	2820	SSE	30	80
Q	2830	SSE	20	85
R	2850	E	3	70
S	2830	N	8	95
T	2840	N	15	95

simple and precise enough to test the validity of the Michaelis-Menten model for a plant community. Mathematically, this method is basically the same as the Lineweaver-Burke method (Cornish-Bowden 1995).

I used linear regression to calculate coefficients of S, $1/\lambda$, B_S and $B_{1/\lambda}$, at a sampling effort of 1–10 squares. I calculated values of r^2 and F (from ANOVA, software Microsoft Excel 5) to estimate goodness-of-fit within this range of sampling effort, that is in terms of interpolation (see also Soberón and Llorente 1993). Subsequently, I used the coefficients S, $1/\lambda$, B_S and $B_{1/\lambda}$ obtained to predict species richness and ISC at a sampling effort of 100 squares (respectively, values of S'_{100} and $1/\lambda'_{100}$). The estimated figures were compared to the actual values observed at the same sampling effort. I took per cent deviation of predicted figures from observed values as extrapolation error, respectively, $EE_S\% = 100 \times (S_{100} - S'_{100})/S_{100}$ and $EE_{1/\lambda}\% = 100 \times (1/\lambda_{100} - 1/\lambda'_{100}) \times \lambda_{100}$, to measure model fitness in terms of extrapolation. Significance of extrapolation was examined by a t-test (Zar 1996).

Results and discussion

The results of applying the Michaelis-Menten model to species and ISC accumulation curves are presented in Table 2A, B. As one can see, interpolation is good in both cases, as demonstrated by similarly high values of r^2 and F. However, extrapolation performance is not good in the case of richness since extrapolation error varies from 0 to values as large as 45%. Hence, despite precise interpolation, the Michaelis-Menten model is not robust to predict S, underestimating it in most cases (mean $EE_S = 21.87\% \pm 8.28$). However, when applied to ISC, the Michaelis-Menten model appeared to be robust and precise, with an average extrapolation error of $-1.51\% \pm 3.15$. A t-test rejected difference of this value from 0.

Fig. 1 shows the results of modelling in two contrasting cases – with least (plot Q); and largest (plot R) EE_S. Curves obtained from all other plots were similar to either of these two examples. Observing the curves on Fig. 1 (and others not shown) one can see that EE_S tends to be larger at lower $1/\lambda_{100}$ relative to S_{100}. A lower ratio of ISC to species richness may indicate a larger proportion of rare species and/or a highly uneven frequency distribution of species. I examined this suggestion by means of dominance-diversity curves. Fig. 2 shows such functions found in the same plots Q and R (see also Fig. 1). These two curves (and others not shown) disclose higher unevenness in the frequency distribution and a longer "tail" of rare species in case(s) of poor extrapolation.

An independent and complementary method to examine plant community structure is dominance analysis (Ohsawa 1984). This method provides a means of distinguishing top and bottom species (see Study area and Methods). Examination of dependence of extrapolation error on the proportion of bottom species showed a pronounced correlation ($r^2 = 0.54$, $F = 23.12$; Fig. 3). Apparently, a large proportion of bottom species significantly contributes to extrapolation error.

From this, I hypothesised that the extrapolated values of richness (S'_{100}) coincided with numbers of top species. Regression analysis produced a high correlation ($r^2 = 0.81$, $F = 123.2$), and a t-test rejected the differ-

Table 2A. Performance of the Michaelis-Menten model as applied to the species accumulation curve (S'_{100} – extrapolated number of species at sampling effort $n = 100$; EE_S – difference between observed and extrapolated values ($S_{100} - S'_{100}$) expressed in % of observed value).

Plot	S_{100}	S	B_S	r^2	F	S'_{100}	EE_S (%)
A	31	22.01	4.89	0.988	716.4	20.99	32.30
B	20	15.30	3.31	0.997	2894.4	14.81	25.97
C	20	12.72	2.88	0.989	847.5	12.36	38.18
D	45	39.69	8.48	0.984	552.7	36.59	18.68
E	41	36.49	8.30	0.991	955.9	33.69	17.82
F	42	34.78	8.27	0.969	285.9	32.13	23.50
G	33	24.15	6.39	0.987	703.4	22.70	31.20
H	27	23.24	4.43	0.991	1020.9	22.26	17.55
I	39	31.64	6.18	0.987	687.9	29.81	23.57
J	32	24.20	5.83	0.990	861.2	22.87	28.53
K	37	34.14	6.94	0.984	538.5	31.93	13.71
L	28	20.31	4.32	0.993	1304.9	19.47	30.45
M	21	17.99	3.99	0.996	2413.3	17.30	17.60
N	22	22.16	5.00	0.986	620.8	21.10	4.08
O	34	27.99	5.88	0.992	1078.6	26.44	22.23
P	27	26.04	5.51	0.983	533.9	24.68	8.60
Q	36	39.26	9.28	0.983	519.1	35.93	0.20
R	27	15.57	3.81	0.979	420.8	15.00	44.45
S	23	18.52	4.78	0.995	1797.7	17.67	23.16
T	25	22.33	5.90	0.986	623.8	21.08	15.67

Table 2B. Performance of the Michaelis-Menten model as applied to the ISC accumulation curve ($1/\lambda'_{100}$ – value of diversity at sampling effort $n = 100$; $EE_{1/\lambda}$ – difference between observed and extrapolated values ($1/\lambda_{100} - 1/\lambda'_{100}$) expressed in % of observed value).

Plot	$1/\lambda_{100}$	$1/\lambda$	$B_{1/\lambda}$	r^2	F	$1/\lambda'_{100}$	$EE_{1/\lambda}$ (%)
A	10.00	9.95	1.39	0.998	5004.218	9.81	1.91
B	7.73	8.09	1.15	0.999	6126.31	8.00	−3.48
C	7.13	7.03	0.90	0.996	2025.706	6.97	2.23
D	19.46	20.24	3.7	0.99353	1223.257	19.52	−0.31
E	12.06	16.68	3.05	0.986	622.3856	13.02	−7.95
F	18.07	18.26	3.70	0.994	1627.628	17.61	2.54
G	9.40	9.71	1.60	0.999	10716.32	9.55	−1.62
H	11.84	11.72	1.44	0.999	11510.22	11.55	2.42
I	17.46	17.83	2.83	0.999	6929.438	17.33	0.72
J	12.06	12.63	2.49	0.997	2590.334	12.32	−2.14
K	19.18	20.42	3.73	0.993	1237.811	19.69	−2.68
L	10.14	10.30	1.56	0.999	8008.427	10.14	−0.05
M	9.80	9.97	1.48	0.996	2254.795	9.83	−0.31
N	11.86	12.84	2.49	0.996	2363.463	12.53	−5.65
O	15.46	15.87	3.01	0.993	1334.348	15.41	0.33
P	14.51	15.99	2.81	0.985	610.7929	15.55	−7.17
Q	16.44	18.80	3.84	0.990	897.7514	18.10	−10.10
R	9.12	8.80	1.51	0.996	2101.248	8.67	4.90
S	10.80	11.00	2.37	0.997	3156.156	10.74	0.53
T	12.28	13.20	3.04	0.994	1535.134	12.81	−4.28

ence between these two values. Fig. 4 shows extrapolated species richness as a function of top species number. Evidently, in grassland communities the Michaelis-Menten model describes with a certain accuracy accumulation of dominant species (or top species as defined

in Study area and Methods; see also Ohsawa 1984), but discriminates against rare (bottom) species.

This selectivity may be employed to assess the number of dominant species when precision is less important than saving time during a survey. However, the
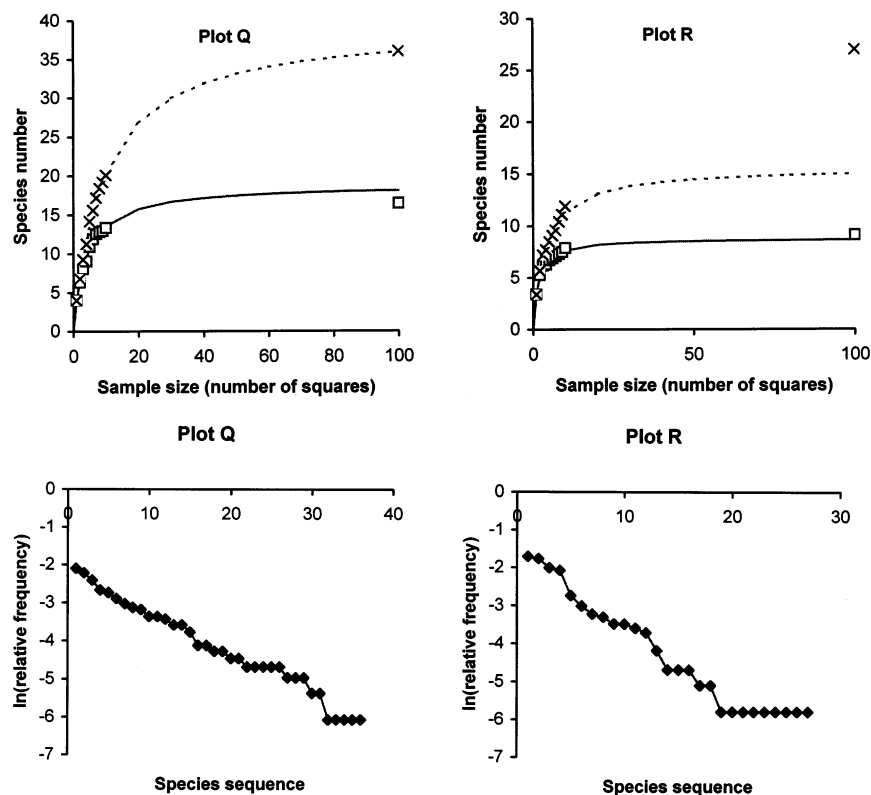

Fig. 1. Modeling of curves: good (Plot Q) and poor (Plot R) performance; crosses – species accumulation, observed values; boxes – ISC accumulation, observed values; dashed line – species accumulation, modelled curve; solid line-ISC accumulation, modelled curve.

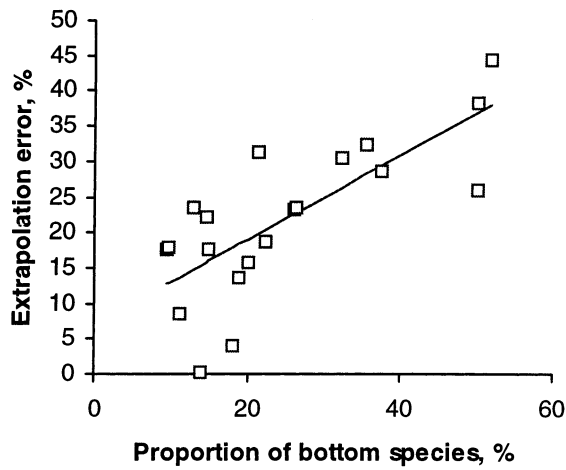Fig. 2. Dominance-diversity curves corresponding to good (A) and poor (B) model performance in Fig. 1.

Fig. 3. Dependence of extrapolation error on the percent share of bottom species; boxes – extrapolation error; solid line – regression.
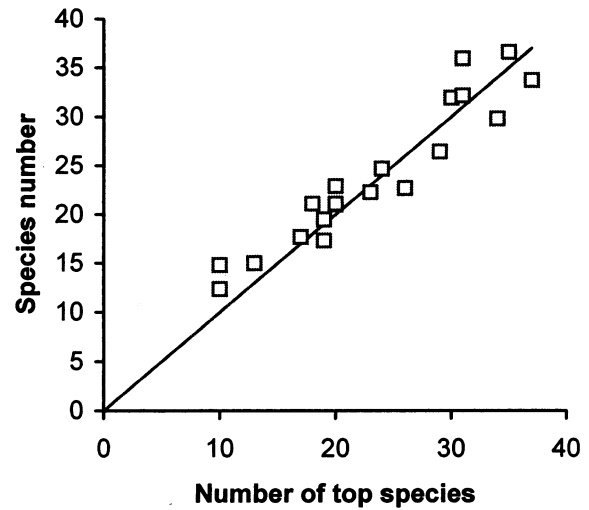

Fig. 4. Extrapolated richness and number of top species in plots; boxes – extrapolated richness in 100 squares; solid line – number of dominant (top) species.

Michaelis-Menten model appears to be precise and robust for predicting frequency-based diversity indices such as ISC, at least when applied to grassland communities. This property may also be employed for calculations of ISC from a small sample. Of course, the estimated diversity will be valid for a community under study to the extent that plots are representative for the community.

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