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Effect of species richness and relative abundance on the shape of the species accumulation curve

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Abstract We explain how species accumulation curves are influenced by species richness (total number of species), relative abundance and diversity using computer-generated simulations. Species richness defines the boundary of the horizontal asymptote value for a species accumulation curve, and the shape of the curve is influenced by both relative abundance and diversity. Simulations with a high proportion of rare species and a few abundant species have a species accumulation curve with a low 'shoulder' (inflection point on the ordinate axis) and a long upward slope to the asymptote. Simulations with a high proportion of relatively abundant species have a steeply rising initial slope to the species accumulation curve and plateau early. Diversity (as measured by Simpson's and Shannon–Weaver indices) for simulations is positively correlated with the initial slope of the species accumulation curve. Species accumulation curves cross when one simulation has a high proportion of both rare and abundant species compared with another that has a more even distribution of abundance among species.

Key words: abundance, diversity, fauna survey, pit-trapping, rarity, reptiles, richness, species accumulation.

INTRODUCTION

A species accumulation curve records the rate at which new species are added with continued trapping effort. The asymptote value of a species accumulation curve is equal to the total number of species present (species richness). The shape of a species accumulation curve depends on the pattern of relative abundance among species sampled (Colwell & Coddington 1994). The pattern of relative abundance or diversity is determined by an interrelationship among species richness, overall abundance and the evenness of species at a site. A species accumulation curve can therefore be a useful tool in understanding species composition for a site as well as in predicting species richness (Palmer 1990, 1991; Soberón & Llorente 1993; Colwell & Coddington 1994; Moreno & Halffter 2000). However, caution needs to be exercised in the prediction of species richness from too small a sample (Palmer 1990; Willott 2001; Thompson *et al.* 2003).

For species accumulation curves to be a useful ecological tool, we must understand how the shape of the curve is affected by changes in species richness, overall abundance and diversity, and the proportion of rare species. Lande *et al.* (2000) indicated that species accumulation curves cross when the community with the lower actual species richness has a higher Simpson diversity index. Lande *et al.* (2000) went on to indicate that the initial slope of the curve is not related to actual species richness, but instead Simpson's diversity. The Shannon–Weaver index of diversity is not suited to comparison among sites because it is biased for small samples, whereas Simpson's diversity has the statistical accuracy for reliable comparison among communities using small samples (Lande *et al.* 2000). Different measures of sampling effort can also influence the shape of the curve (Moreno & Halffter 2001; Willott 2001).

In the accompanying paper (Thompson *et al.* 2003) we report on which of the available species accumulation curve models provides the best fit for field sampling of reptile communities, how the shape of the curve varies for the different sites, and how this is related to species richness and measures of diversity. The purpose of the present paper is to explain, using computer simulations, how species richness, the proportion of rare species, overall abundance and measures of diversity are reflected in the shape of species accumulation curves.

METHODS

We used a software program written and compiled in Visual Basic V6 to model trapping effort (e.g. pit-trap days or number of individuals caught) for a defined group of species, each with a predetermined number of individuals and probability for being caught. Initially, each individual for each species was examined, and

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determined to have been captured (or not captured) based on the probability of capture for that species and a random number generated for that individual. Then, the order of capture was randomized, for those individuals that were determined to have been captured. This random process was repeated for each unit of effort, which we call a trap-day. Ten iterations were generated for each simulation, and the results were averaged to reduce random sampling variation. The total number of species for most of the simulations was 24, which approximated the number of species we caught in a biotope for 20 nights of trapping (Thompson *et al.* 2003). The probability of catching an individual of any species was held constant in all simulations (0.001). The results of these simulations enabled us to (i) compare the shape of species accumulation curves when the number of individuals for each species was the same, that is, *J* (evenness) = 1.0

Table 1. Data sets for eight simulations with different species richness, abundance and diversity that are used in the computation of species accumulation curves that are plotted in Figs 1–6

	Simulations							
Species	A	B	C	D	E	F	G	H
1	200	160	200	240	1	20	10	1
2	200	160	200	240	18	20	10	11
3	200	160	200	240	35	20	10	21
4	200	160	200	240	56	20	10	31
5	200	160	200	240	73	20	10	41
6	200	160	200	240	90	20	10	51
7	200	160	200	240	107	190	10	61
8	200	160	200	240	124	190	10	71
9	200	160	200	240	141	190	10	81
10	200	160	200	240	158	190	10	91
11	200	160	200	240	175	190	10	101
12	200	160	200	240	192	190	10	111
13	200	160	200	240	209	190	10	121
14	200	160	200	240	226	190	10	131
15	200	160	200	240	243	190	10	141
16	200	160	200	240	260	190	400	151
17	200	160	200	240	277	190	400	161
18	200	160	200	240	294	190	400	171
19	200	160		240	311	400	450	181
20	200	160		240	328	400	600	191
21	200	160		240	345	400	600	201
22	200	160		240	362	400	600	211
23	200	160		240	379	400	600	221
24	200	160		240	396	400	600	2247
25		160						
26		160						
27		160						
28		160						
29		160						
30		160						
SR	24	30	18	24	24	24	24	24
I	4800	4800	3600	5760	4800	4800	4800	4800
P_t	24	30	19	24	22	22	–	21
P_{t50}	24	30	18	24	22	22	20	21
P_i	24	30	19	24	22	20	22	29
P_{i250}	24	30	19	24	22	21	13	28
S	0.96	0.97	0.94	0.96	0.94	0.94	0.89	0.76
H	3.18	3.40	2.89	3.18	2.97	2.91	2.34	2.25
J	1.00	1.00	1.00	1.00	0.93	0.92	0.73	0.71
r_t^2	0.999	0.996	0.988	0.976	0.993	0.995	0.970	0.985
r_i^2	0.999	0.999	0.999	0.999	0.999	0.999	0.994	0.998

Values for 1–30 species are total numbers of individuals in the population. *SR*, species richness; *I*, total number of individuals; P_t, predicted asymptote based on trap days; P_{t50}, predicted number of species caught after 50 trap days; P_i, predicted asymptote based on number of individuals caught; P_{i250}, predicted number of species caught after 250 individuals caught; *J*, evenness index; *S*, Simpson's diversity index; *H*, Shannon–Weaver diversity index; r_t^2, beta-P model adj. r^2 for trap data; r_i^2, beta-P model adj. r^2 for individuals caught data.

(Tramer 1969); and (ii) examine the shape of the curve when we altered the number of individuals for each species (i.e. varied species evenness/rarity).

To compare the shape of species accumulation curves with different species abundance or richness, when the evenness (or rarity) of species was identical, we first computed trapping results for 24 species, each with 200 individuals and all individuals with the same probability (0.001) of being caught each day for 20 days (simulation A). Increasing or decreasing the probability of an individual being caught has an equivalent effect on capture results as altering the number of traps per day. We then repeated the computation (simulation B) with the number of individuals available for capture reduced for each species to 160 and the number of species increased to 30 (the total of 4800 individuals available for capture was the same as for the first simulation). For the third simulation (C), we left the number of individuals per species at 200, the same as in the first simulation, but reduced the number of species from 24 to 18, giving a total of 3600 individuals available for capture (see Table 1 for data). For the fourth simulation (D), we left the number of species and evenness the same as for simulation A but increased the number of individuals per species available to be caught (200–240; Table 1).

To examine how the shape of the species accumulation curve changed when the evenness (or rarity) of species varied, we compared five sets of simulations (A, E, F, G and H). The total number of individuals available to be caught was 4800, the total number of species was 24, and the probability of each individual being caught was 0.001. The relative abundance for each of the species was altered in each of the simulations to change the evenness and diversity. Data for each of the five species accumulation curves are shown in Table 1.

Simpson's and Shannon–Weaver (H) diversity indices (Hayek & Buzas 1997;

$$\text{Simpson} = 1-\sum_{i=1}^{S} p_i^2;$$

$$\text{Shannon-Weaver} = -\sum_i p_i \ln(p_i)$$

were calculated for each of the simulations (A–H; Table 1). Species accumulation curves using both the number of trap-days and the number of individuals caught were calculated using the Beta-P model (Flather 1996; Lande *et al.* 2000) as this was the model that best matched our field data for reptiles in the arid areas of Western Australia (Thompson *et al.* 2003). Non-linear regression equations for each of the curves were determined using NLREG (Sherrod 1991) software. Adjusted r^2 values (to indicate 'goodness-of-fit') and asymptotes are reported for each of the data sets. Smoothed curves were drawn from the Beta-P non-linear regression equations to display the shape of the curves.

RESULTS AND DISCUSSION

The shape of species accumulation curves changed with species richness, and when species richness was

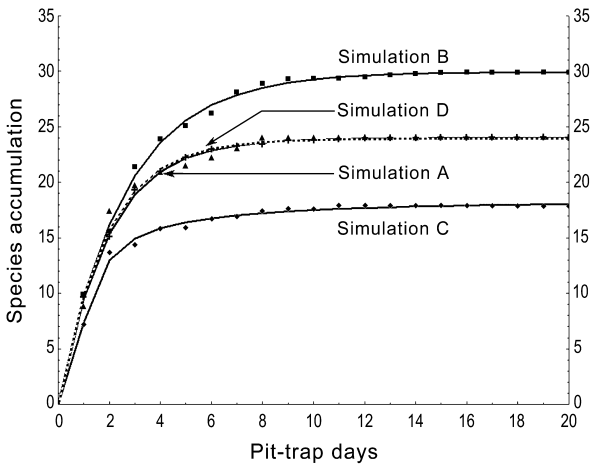

Fig. 1. Species accumulation curves for simulations A, B, C and D (data in Table 1) with trap-days as the measure of effort. Dots are actual data points, smoothed lines are the species accumulation curves calculated using the Beta-P model; *J*, evenness index; *S*, Simpson's diversity index; *H*, Shannon–Weaver diversity index. Simulation B, *J* = 1.0, *S* = 0.97, *H* = 3.40. Simulation D, *J* = 1.0, *S* = 0.96, *H* = 3.18. Simulation A, *J* = 1.0, *S* = 0.96, *H* = 3.18. Simulation C, *J* = 1.0, *S* = 0.94, *H* = 2.89.

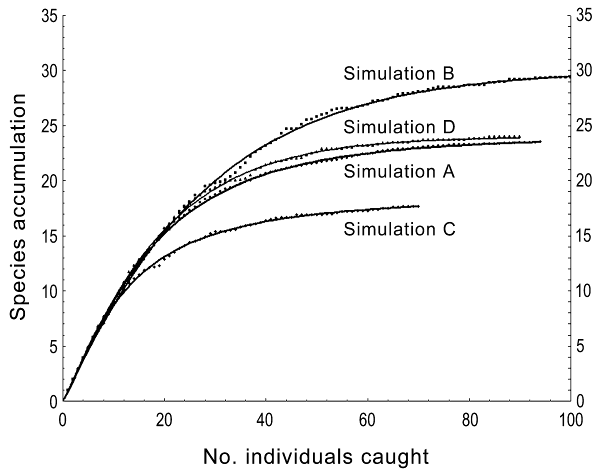

Fig. 2. Species accumulation curves for simulations A, B, C and D (data in Table 1) with the number of individuals caught as the measure of effort. Dots are actual data points, smoothed lines are the species accumulation curves were calculated using the Beta-P model; *J*, evenness index; *S*, Simpson's diversity index; *H*, Shannon–Weaver diversity index. Simulation B, *J* = 1.0, *S* = 0.97, *H* = 3.40. Simulation D, *J* = 1.0, *S* = 0.96, *H* = 3.18. Simulation A, *J* = 1.0, *S* = 0.96, *H* = 3.18. Simulation C, *J* = 1.0, *S* = 0.94, *H* = 2.89.

held constant but the proportional abundance of species was altered (and thus diversity and evenness values varied among simulations). The species accumulation curve for simulation A, with 24 species and 200 individuals per species ($J = 1.0$) is used as a reference for most comparisons.

Changing number of species and individuals per species

Effects of changing either the number of species (24–18; A and D) while holding the number of individuals per species constant, or reducing the number of individuals per species (200–160; A and B) and increasing the number of species (24–30) so that the total number of individuals in each simulation is unchanged (4800), or holding the number of species constant (24; A and D) and changing the number of individuals per species (200–240; D), are shown in Fig. 1 (based on trap-days) and Fig. 2 (based on number of individuals caught). The asymptotes for simulations A and D with the same number of species are the same, and all asymptotes closely approximate the actual number of species in each of the simulations. Species accumulation curves A to D have reached the asymptote after 20 trap days.

The general shape for the species accumulation curves A, B and C appears similar in Figs 1 and 2, but to compare their shapes better they were normalized to 100% of species richness (Fig. 3) using trap-days as the measure of effort. The most noticeable difference among these three normalized curves is the lesser initial slope of species accumulation curve B compared with curves A and C; this reflects the lower number of individuals per species (160 *vs* 200) available to be caught.

It is apparent from an inspection of Fig. 2 that when the number of individuals is the same for each species (i.e. $J = 1.0$) then randomly capturing approximately 2% (i.e. 96/4800) of the total number of individuals in the community provides a complete inventory of species. This evenness never occurs in nature so this information is of theoretical interest only.

Alternative measures of trapping effort

Altering the measure of effort alters the shape of the species accumulation curves. This can be seen by comparing simulations A and D in Figs 1 and 2. In Fig. 1 (trap-days as the measure of effort), species accumulation curves for A and D are very similar; however, in Fig. 2 (number of individuals caught as the measure of effort), the initial rise of species accumulation curve for simulation D goes higher than for simulation A, with both species accumulation curves plateauing at 24. The more obvious difference in curve shape between the two measures of effort is for simulation H (Figs 4 and 5). The high predicted species richness (i.e. asymptote; 29) for simulation H (using the number of individuals caught as the measure of effort) indicates that the non-linear regression program did not accurately estimate species richness because the

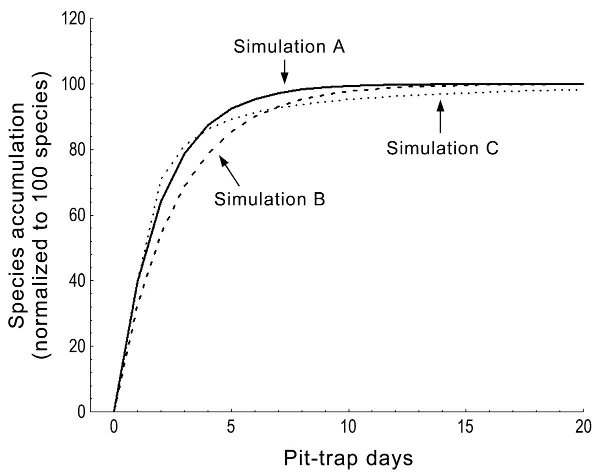

Fig. 3. Species accumulation curves for simulations A, B and C (data in Table 1) with trap-days as the measure of effort, normalizing the number of species caught after 50 trap days to 100 to show shape differences for the curves. Simulation A, 24 species, 200 individuals per species, $n = 4800$. Simulation C, 18 species, 200 individuals per species, $n = 3600$. Simulation B, 30 species, 160 individuals per species, $n = 4800$.

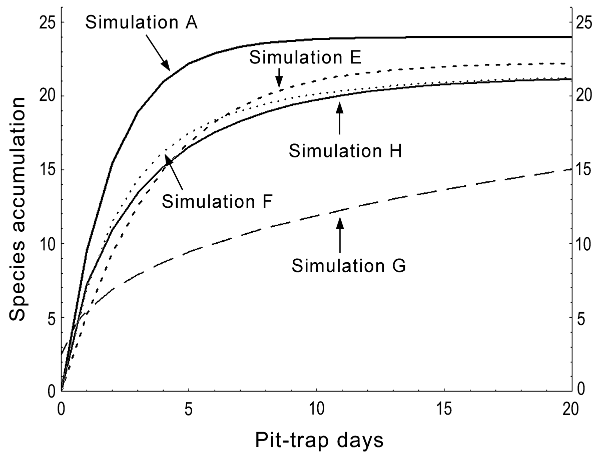

Fig. 4. Species accumulation curves for simulations A, E, F, G and H (data in Table 1) with trap-days as the measure of effort. Species accumulation curves were calculated using the Beta-P model; J, evenness index; S, Simpson's diversity index; H, Shannon–Weaver diversity index. Simulation A, $J = 1.0$, $S = 0.96$, $H = 3.18$. Simulation E, $J = 0.93$, $S = 0.94$, $H = 2.97$. Simulation H, $J = 0.71$, $S = 0.76$, $H = 2.25$. Simulation G, $J = 0.73$, $S = 0.89$, $H = 2.34$. Simulation F, $J = 0.92$, $S = 0.94$, $H = 2.91$.

plateauing of the species accumulation curve has not commenced to level out sufficiently (Fig. 5). In contrast, when trap-days are used as the measure of effort the predicted species richness is an underestimate (21) of actual species richness (Fig. 4). For simulation H, additional trapping (to catch more individuals) is required so the plateau for the species accumulation curve is well established to obtain an accurate estimate of species richness using either measure of trapping effort. More trapping effort is required for simulation H than the other simulations (except G) to estimate species richness because of the proportionally higher number of rare species. The evenness index is lowest for simulation H (0.71) mostly because of the large discrepancy between the species with the highest abundance and the relatively low number of individuals for the other species.

Species accumulation curve G differs most from the other curves (Figs 4 and 5) for both measures of effort (trapping days and number of individuals caught). The asymptote (not reached in Fig. 4) is 42 534 species when plotted with number of trap-days, which is obviously incorrect. Insufficient trapping effort to catch enough of the rare species (15 species with 10 individuals per species) has meant the species accumulation curve has yet to level out sufficiently to provide an accurate estimate of species richness. This is evident in Fig. 6, where the smoothed species accumulation curve calculated using Beta-P overlays the actual data points. The slow but continuous increase in the regression line after the inflection point reflects the considerable trapping effort required to capture even one representative of the high number of relatively rare species in this simulation. At 250 caught individuals, only 13 of the 24 species have been captured, compared with the other simulations that are all within one species of the actual species richness (except H as discussed above).

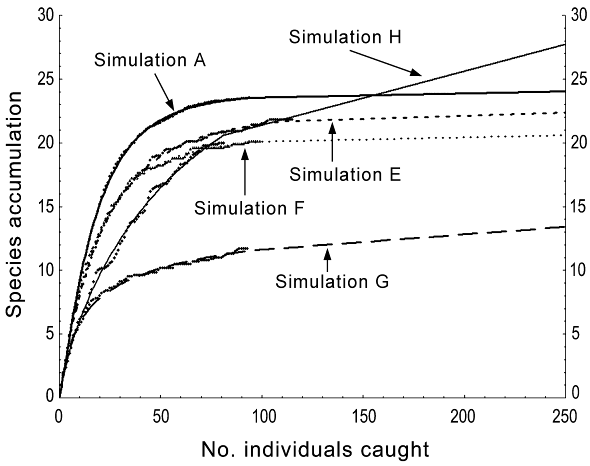

Fig. 5. Species accumulation curves for simulations A, E, F, G and H (data in Table 1) with number of individuals caught as the measure of effort. Species accumulation curves were calculated in the Beta-P model; J, evenness index; S, Simpson's diversity index; H, Shannon–Weaver diversity index. Simulation H, $J = 0.71$, $S = 0.76$, $H = 2.25$. Simulation A, $J = 1.0$, $S = 0.96$, $H = 3.18$. Simulation E, $J = 0.93$, $S = 0.94$, $H = 2.97$. Simulation F, $J = 0.92$, $S = 0.94$, $H = 2.91$. Simulation G, $J = 0.73$, $S = 0.89$, $H = 2.34$.

Crossing species accumulation curves

Species accumulation curves E and F, which cross, have similar diversity indices. In Fig. 4, the curve for simulation F has a higher initial slope than curve E, reflecting the relatively high abundance of a few species (e.g. six species with 400 individuals). A greater effort is required to capture a representative of the six species with a relatively low abundance (i.e. 20 individuals per species) in simulation F, than for the rarest six species in simulation E, as a consequence at 20 trap-days the number of species recorded for simulation F is less than for simulation E. Similarly, after 250 individuals are caught, 22 species are recorded at E and 21 species at simulation F (Fig. 5). The greater effort required for simulation F compared with simulation E to collect all species means that the slope of the curve will be slightly steeper for F than for E after the inflection point.

Lande *et al.* (2000) suggested that species accumulation curves (canopy traps (butterflies) × days) cross when the community with the lower actual species richness has a higher Simpson diversity index. Our simulations F and E have the same actual species richness (24) and very similar Simpson's diversity indices (0.94), but their species accumulation curves nevertheless cross (Figs 4 and 5). It is therefore

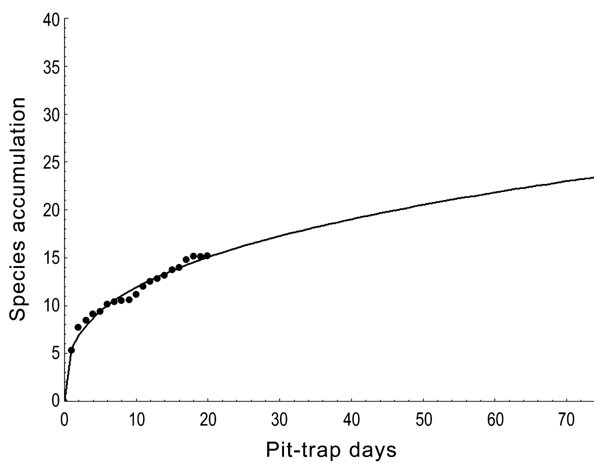

Fig. 6. Species accumulation curve for simulation G, showing actual data points and the smoothed species accumulation curve were calculated using the Beta-P model projected to 75 pit-trap days to demonstrate the effect that a high proportion of rare species has on the trapping effort required before a species accumulation curve can be used to accurately estimate species richness.

apparent there are circumstances other than those described by Lande *et al.* (2000) where the species accumulation curves cross.

Diversity and slope of the species accumulation curve

Lande *et al.* (2000) went on to indicate that the initial slope of the curve is not related to actual species richness, but instead Simpson's diversity. Although we present only a small sample (simulations A, B, C, D, E, F, G and H), we found a highly significant correlation between Simpson's index and the initial slope of the species accumulation curve using the first 10 individuals caught ($r = 0.76$, $P < 0.05$). There is also a significant positive correlation between the Shannon–Weaver index of diversity and the initial slope of the species accumulation curve using the first 10 individuals caught (Fig. 5; $r = 0.91$, $P < 0.01$). The slope of the initial curve is therefore positively related to diversity.

Summary

The shape of species accumulation curves is influenced by species richness and relative abundance. Species richness alters the asymptote, as would be expected. Sites with a high proportion of rare species and few abundant species have a species accumulation curve with a low inflection point on the *y*-axis and a long upward sloping line to the asymptote. For these sites, a much greater trapping effort is required to capture a sufficient number of the rare species for the species accumulation curve to plateau and accurately predict species richness. In contrast, sites with a high proportion of relatively abundant species have a steep rising initial slope, plateau early and provide an accurate estimate of species richness with less trapping effort than when there is a higher proportion of rare species. Sites with high diversity (as measured by Simpson's and Shannon–Weaver indices) have steeper initial slopes for their species accumulation curves. Species accumulation curves cross when the community with the lower actual species richness has a higher Simpson's diversity index (Lande *et al.* 2000) and when one site has a high proportion of both rare and abundant species compared with another site that has a more even distribution of abundance among species, but this difference need not be reflected in diversity or evenness indices.

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