TREE SPECIES–AREA AND SPECIES–DIAMETER RELATIONSHIPS AT THREE LOWLAND RAIN FOREST SITES IN SUMATRA

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RENNOLLS, K. & LAUMONIER, Y. 1999. **Tree species–area and species–diameter relationships at three lowland rain forest sites in Sumatra.** Data from three forest sites in Sumatra (Batang Ule, Pasirmayang and Tebopandak) have been analysed and compared for the effects of sample area cut-off, and tree diameter cut-off. An 'extended inverted exponential model' is shown to be well suited to fitting tree-species–area curves. The model yields species carrying capacities of 680 for Batang Ule, 380 species for Pasirmayang, and 350 for Tebopandak (tree diameter ≥ 10 cm). It would seem that in terms of species carrying capacity, Tebopandak and Pasirmayang are rather similar, and both less diverse than the hilly Batang Ule site. In terms of conservation policy, this would mean that rather more emphasis should be put on conserving hilly sites on a granite substratum. For Pasirmayang, with tree diameter ≥ 3 cm, the asymptotic species number estimate is 567, considerably higher than the estimate of 387 species for trees with diameter ≥ 10 cm. It is clear that the diameter cut-off has a major impact on the estimate of the species carrying capacity. A conservative estimate of the total number of tree species in the Pasirmayang region is 632 species! In sampling exercises, the diameter cut-off should not be chosen lightly, and it may be worth adopting field sampling procedures which involve some subsampling of the primary sample area, where the diameter cut-off is set much lower than in the primary plots.

Key words: Species–area curves - species–diameter curves - non-linear modelling

RENNOLLS, K. & LAUMONIER, Y. 1999. **Kaitan antara spesies dan luas pokok dengan spesies dan garis pusat pokok di tiga tapak hutan hujan tanah pamah di Sumatera.** Data daripada tiga tapak hutan di Sumatera (Batang Ule, Pasirmayang dan Tebopandak) dianalisis dan dibandingkan untuk mendapatkan kesan sampel bagi potongan kawasan dan potongan garis pusat pokok. Model eksponen songsang diperluas didapati sangat sesuai dengan lengkuk kawasan spesies pokok. Model ini menghasilkan spesies dengan daya muat membawa sebanyak 680 spesies bagi Batang Ule, 380 spesies bagi Pasirmayang, dan 350 spesies bagi Tebopandak (garis pusat pokok ≥ 10 cm). Nampaknya dari segi keupayaan spesies, Tebopandak dan Pasirmayang lebih kurang sama, dan kedua-duanya kurang kepelbagaiannya berbanding dengan

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tapak Batang Ule yang berbukit. Dari segi polisi pemuliharaan, ini bermakna bahawa penekanan perlulah diberikan untuk memulihara tapak berbukit di atas substrata granit. Bagi Pasirmayang, dengan garis pusat ≥ 3 cm, anggaran bilangan spesies asimtot ialah 567, lebih tinggi daripada anggaran 387 spesies bagi pokok bergaris pusat ≥ 10 cm. Jelas bahawa potongan garis pusat mempunyai kesan utama terhadap anggaran daya muat membawa spesies tersebut. Satu anggaran konservatif mengenai jumlah spesies pokok di kawasan Pasirmayang ialah 632 spesies! Dalam pensampelan, potongan garis pusat mestilah dipilih dengan berhati-hati. Penggunaan prosedur pensampelan yang melibatkan beberapa subpensampelan kawasan sampel primer, iaitu potongan garis pusat disediakan jauh lebih rendah daripada plot primer.

Introduction

One of the primary concerns of floristic specialists in studying a particular forest region is the total number of species in the region (Peet 1975, Hubbell 1979, Hubbell & Foster 1983, Magurran 1988, Turner *et al.* 1997). Rennolls and Laumonier (1998) showed that the number of species in a plot is one of the primary dimensions of species diversity in two distinct forest sites in Sumatra, Batang Ule and Pasirmayang. It is well known that the observed number of species, and indeed any calculated measure of diversity, will depend on the area of the sample plot (Fisher *et al.* 1943, Pielou 1975). As the area of the sample plot increases, the number of species observed, and any of the measures of diversity will increase. The traditional ecological question is therefore, how many species would be observed on a very large forested region, of which the sampled area is typical (Kent and Coker 1992). A similar question could be asked of measures of diversity (Boyle & Boontawee 1995, Vanclay 1996), but this paper is concerned solely with the estimation of the total number of species. There are two standard approaches: (i) to fit a suitable model to the species frequency distribution (usually negative binomial or lognormal), and to estimate the number of undetected species from the truncated part of these distributions, (ii) to extrapolate the associated collector's curves (i.e. the species–area curves).

In practical field terms it is necessary to use a minimal diameter cut-off, because of the very large number of trees of small diameter. Figure 1 is a plot of log_e [log_e(*number of observed trees*)] against the diameter cut-off, d_{min}, for the Pasirmayang site of this study. It shows how the total number of trees observed varies with the diameter cut-off. The very high rate at which the number of observed trees increases with decreasing minimal diameter is of course the reason that a reasonably high diameter cut-off is adopted in empirical observational studies. Visual extrapolation in Figure 8 to d_{min} = 0 gives an maximal estimate for the intercept of about 2.3, corresponding to a total stocking on the 3-ha site of about 21 500 trees [= exp(exp(2.3))].

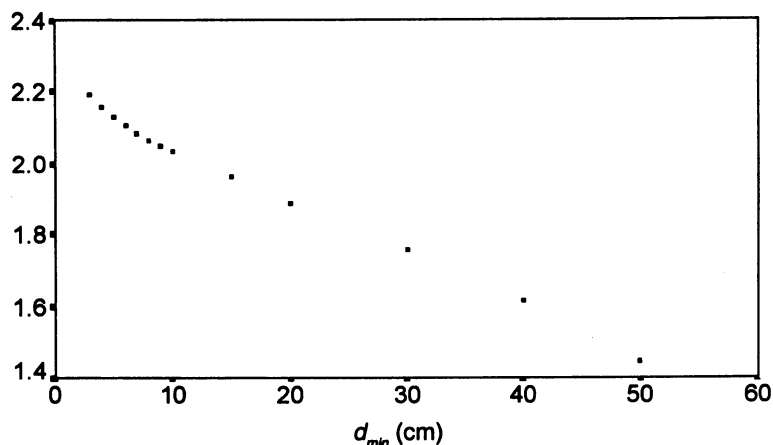**Figure 1.** Pasirmayang: plot of $log_e [log_e (number\ of\ observed\ trees)]$ v d_{min}

It is also clear that use of a minimum diameter cut-off when observing the trees in a sample area will result in an underestimate of the species carrying capacity for all trees. Little attention has been paid to the effect of the choice of the selection criterion for trees on the estimation of the total number of tree species. Usually a minimal size criterion is used, chosen to reflect the part of the forest ecosystem which is of primary concern. Hubbell and Foster (1983) used a minimum diameter of 20 cm, since this reflected their interest in the trees that are part of the upper canopy of the forest. Though the qualitative effect of the use of a diameter cut-off is obvious, it does not seem that quantitative analysis of this diameter cut-off effect has been conducted in observational studies of the tropical rain forests. However, if concern is with the biodiversity of the whole tropical rain forest ecosystem, such arbitrary cut-offs obscure the true range of tree species diversity that occurs. It is therefore of interest to investigate the effect of minimal cut-off diameter on the number of tree species that are observed. Initially the species–area curves for the three sites are analysed by fitting non-linear statistical models for trees with diameter ≥ 10 cm and the extrapolative estimate of the total species carrying capacities determined for each site.

The Pasirmayang site is of area 10 ha, with a 3-ha core plot in which trees have been observed and species and spatial locations recorded, for trees with diameters down to 3 cm. The other sites considered in this paper, Batang Ule and Tebopandak, have species and locations of trees recorded only for trees with diameter ≥10 cm, a diameter cut-off that is typical in many forest inventories or vegetation surveys in tropical forest areas. Other reported studies have used diameter cut-offs of 20, 30 or even 50 cm. Clearly the observed numbers of species in these studies with different diameter cut-offs are not comparable, and neither are the carrying capacities estimated from the use of species–area curves.

The data from the Pasirmayang site (Laumonier 1997) have been used to evaluate the effect of varying the diameter cut-off, and extrapolative methods have been used to estimate the carrying capacity of the site for trees of all diameters. Finally an attempt is made to obtain combined models of the species–area–diameter relationship.

The study site

The data from Tebopandak were collected as part of a Phase-I implementation of the Forest Inventory and Monitoring Project (FIMP) which was designed to obtain both traditional forest inventory data and forest diversity information. The sampling plan uses a standard field assessment plot of 100 m by 10 m directed along the line of maximal topographic slope. In some instances it is not possible because of site conditions to obtain a 100-m field assessment plot, and a 50-m plot is then used. The rationale of the orientation of the plot is that such a choice will maximise the number of environmental conditions encountered, and the number of tree species detected. Though this is a standard floristic sampling strategy, it does pose some problems in constructing unbiased regional forest inventory estimates. A method for doing this has been described in Rennolls (1997a, b).

Data from Batang Ule and Pasirmayang were collected prior to the FIMP Phase-I study. For both these sites the data used in this paper are from a 300 m by 100 m (3 ha) assessment area. In order to allow comparisons between Tebopandak and these sites the 3-ha assessment areas have been divided into 30 100 m by 10 m 'sample-plots' for the purpose of analysis. Other sub-plot choices, such as 10 m by 10 m, have been used in analyses not reported in this paper.

Batang Ule

The sampled area at Batang Ule is rectangular of dimensions 300 m by 100 m, with an area of 3 ha on which 1885 trees of diameter 10 cm or over are observed, being from 502 different species (Trichon 1996). The site is very heterogeneous, including a valley region, steep slopes, and narrow ridges, (see Lieberman *et al.* 1996, for comparisons). Illustration of the topography, and the way in which diversity measures vary with topography can be found in Rennolls and Laumonier (1999). The plot has been oriented so that the 300-m side of the plot is along the line of maximal topographic gradient. For the purposes of species–area analysis the site has been sub-divided into 30 sub-plots of dimensions 100 m by 10 m, oriented across the line of maximum topographic gradient. The sub-plots are therefore approximately on topographic contours, and are essentially homogeneous, within themselves, but there will be a wide between-plot variation generated by the wide variation in topography over which the plots have been placed. The lower order plots are in the valley, the middle order plots are on a steep slope rising to narrow ridges on which the higher numbered plots lie.

Pasirmayang

The Pasirmayang study site is flat. Since the diversity analysis of the Batang Ule data (Rennolls & Laumonier 1999) showed an increased species diversity associated with ridge plots, it might be expected that the Pasirmayang site would show species diversity measures, including species count, similar to that observed in the flat areas of Batang Ule. The measurements in Pasirmayang are made on all trees down to a diameter of 3 cm. In order to allow a valid comparison between estimates of the species carrying capacities at the three sites considered, the data at Pasirmayang are first analysed using a diameter cut-off of 10 cm, the same as was used at Batang Ule and Tebopandak.

Tebopandak

In the Tebopandak region 45 plots have been assessed, 26 are 100 × 10 m, 19 are 50 × 10 m. All were oriented along the line of maximal topographic gradient. A total of 300 species were observed, with a tree diameter cut-off of 10 cm. There were a considerable number of unidentified trees, and these have been lumped into a single species for the purposes of the analysis in this paper. No account has been taken of this in the species–area analysis (see Rennolls 1997a, b and Rennolls & Laumonier 1999, for further analysis and discussion of these issues).

Species–area curves

Ecologists generally obtain their species–area curves by repeatedly halving the study area considered, so that the sequence of areas considered forms a geometric progression. If the area variable in the species–area analysis is to be log-transformed, then this will result in log (area) values which are evenly spaced. Such evenly spaced data are well suited for testing the adequacy of fit of a range of models in terms of log(area), the best of which may then be used for extrapolative purposes. Such an approach focuses consideration predominantly on the numbers of species observed in very small sub-areas. When the main objective of the study of species–area curves is for extrapolation to very high areas this focus on small sub-areas is not statistically efficient. In order to improve the quality of extrapolative predictions more emphasis should be given to the number of species observed on large sub-areas. Hence the conventional area-halving procedure has not been followed here. The area variable has been left untransformed, and the area values in the species–area analysis have been formed by a cumulation of the areas of a number of sub-plots which have an area typically of 0.1 ha.

The way in which a set of sub-plots is selected needs some care. The assumptions of the species–area curve method need to be taken into account. The sample area will usually contain a number of zones which environmentally differ, based for example on elevation, gradient, soil, etc. The extrapolation of the species–area curves allows an estimate of the number of species which would be found in an

(hypothetical) region of area greater than the sample area which has the same environmental sub-zones as the sample area occurring in the same ratio. For it to be valid to extrapolate the fitted species–area curve it is necessary that each sub-area of the sample area should also contain the same environmental sub-zones in the same ratio. However, the nature and areas of all possible relevant sub-zones in the sample area will not in general be known. Hence it is not possible to ensure that the sub-areas strictly satisfy the requirement that they should follow the environmental-zone ratios of the sample area. In such a situation one approach to ensuring that the sub-area is representative of the sample area is to form the sub-area from a random sub-sample of plots in the sample area.

The "wrong" species–area curve

Figure 2 shows the species–area curve for the 3-ha sample area at Batang Ule for the sub-plots of cumulative area $i*0.1ha$; $i = 1,2,...,30$ when i follows a plot ordering from the valley, up the slope, over the ridge. There is an apparently almost linear increase in the number of species with plot area. However, since the plot index spans the topographic gradient along which new species are expected to be encountered, the near linearity of the species–area curve is not surprising. A cumulative sub-plot constructed from this (natural) ordering of plot numbers is not representative of the whole variability in topography that is present on the whole of the study site. Hence the species–area curve constructed from the cumulative plots from this natural plot ordering is inappropriate for species–area analysis and extrapolation.

Randomised species–area curves

If a sub-area of the 3-ha site is to be made up of a number of the 0.1-ha sub-plots, then in order for the sub-area to be "representative" of the whole of the Batang Ule sample area, the sub-plots may be chosen randomly from the 30 available sub-plots. This can be achieved for all sub-areas of areas from 0.1 ha to 2.9 ha by forming the cumulative sub-areas using a plot numbering formed by a random permutation of the original (natural) plot ordering. There are 30! different permutations of the original plot ordering, each of which will result in a different observed species–area curve. One of these will be the original (natural) plot ordering, which we have seen is not suitable for use in species–area curve analysis. However, in a relatively small subset of random permutations each is likely to achieve a high degree of "mixing-up" of the natural plot ordering, and hence ensure that each of the chosen sub-areas is representative (in the random sampling sense) of the whole sample area. A set of ten random permutations has been selected from the set of all permutations. This results in ten randomly sampled sub-areas at each area from 0.1 ha to 2.9-ha, in 0.1-ha steps. Results for Batang Ule are shown in Figure 2. (Software in Visual Basic for Excel has been written for the generation of the permuted data, and may be obtained from the first author.) Clearly the original

species–area plot is anomalous. The permuted-plot-order curves give the fairest indication and hence in the analysis given below, only the permuted-plot-order data are used. A larger sample could have been selected, but it was considered that the ten sample species–area curves gave an adequate representation of the trend and variability for estimation purposes.
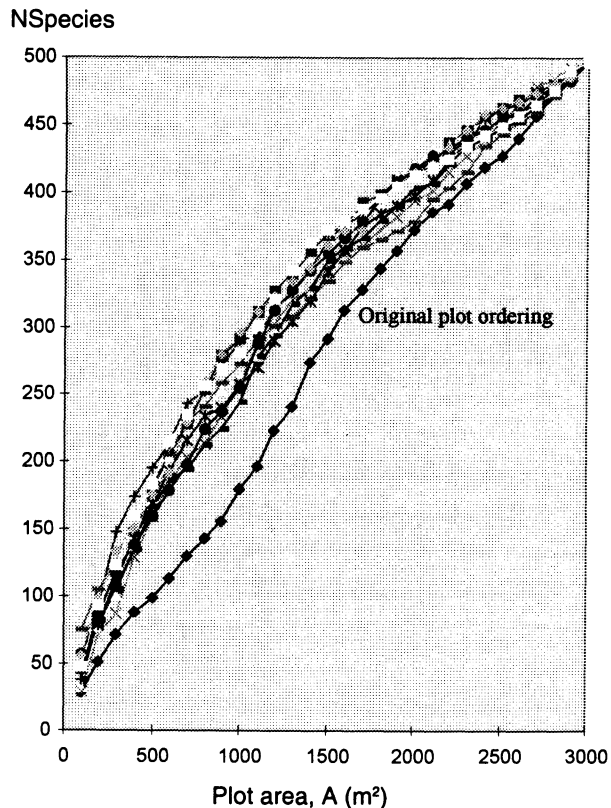

Figure 2. Batang Ule: species–area curves for the original and ten
random plot re-orderings, (d_{min} = 10 cm)

Statistical analysis

The ten randomised species–area curves of Figure 2 for Batang Ule pass through two fixed points. First, the origin, for the observed species count is necessarily zero when A= 0. A model of the species–area relationship should be constrained to pass through the origin. Second, when A = 3.0 ha the observed species count is 502. It is possible that the species–area relationship could also be constrained to go through the (3.0, 502) fixed point of the randomised species–area curves. However, the upper fixed point is merely a result of the actual area that is sampled.

There are an infinite number of possible sample areas which could have been selected from the larger (hypothetical) region to which we wish to extrapolate. They would yield differing values of the number of species observed in the whole 3-ha area. The variation in the numbers of species observed in specified-area sub-areas of the 3-ha plot contains information on the variability of the number of species that would be observed if the whole 3-ha plot had been re-sampled from the hypothetical (super-) population of such plots. In fact, the variance of the number of observed species will increase with increasing sampled area, and this is illustrated in Figure 1 by the divergence of the randomised species–area curves as the area of the sub-area increases from A = 0.

In this paper we have adopted a compromise approach which uses ordinary least squares (OLS) to estimate the species–area relationship from the randomised species–area curves. This is equivalent to giving equal weighting to all the data points on the randomised species–area curves. OLS is the maximum likelihood method of estimation if the data have a homogeneous and independent error structure. It is expected that the use of OLS in the fitting of species–area relationships will result in fitted models which are reasonably unbiased. However, the standard errors of the estimated model parameters should not be taken at face value, since the assumptions under which they would be valid, i.e. homogeneity and independence, are not satisfied. They may be useful as a guide to the relative accuracy of estimation on the different sites considered.

Species–area model

Both the inverted exponential model and the "collector's curve" (Pielou 1975, page 39) were found to be unsatisfactory in fitting the species–area curves. An 'extended inverted exponential model' of the form

$$NSpecies = K1*[1-exp(-K2*((Area/1000)**K3))] \qquad (1)$$

was found to be an adequate representation of the species–area relationships at all three study sites, in terms of residual analyses. The parameter $K1$ represents the asymptotic species carrying capacity.

Species–area results

Batang Ule

Model (1) was fitted to the randomised species–area curves for Batang Ule (tree diameter ≥ 10 cm) shown in Figure 2 using ordinary least squares (OLS) and gave the parameter estimates shown in Table 1.

Table 1. Parameter estimates for Batang Ule for model (1), (d_{min} =10 cm)

Parameter	Estimate	Asymptotic std. error	Asymptotic 95 % confidence interval	
			Lower	Upper
K1	675.6	22.8	630.6	720.5
K2	0.52	0.024	0.47	0.57
K3	0.83	0.017	0.80	0.87

From Table 1 it can be seen that the estimated total number of species in an area as characterised by the Batang Ule plots is 676 [approximate 95% confidence interval (631,720)] which may be compared with the 502 observed species on the site.

Pasirmayang

Tree diameter ≥10 cm

The natural-ordering and randomised species–area curves for Pasirmayang are shown in Figure 3, for trees with diameter greater than or equal to 10 cm. Note that since this site is flat, and there is no environmental gradient, the sequentially ordered sub-plots produce a species–area curve which is not distinguishable from the species–area curves from the randomised plot sequences. Hence in subsequent analysis, all the eleven species–area curves given in Figure 3 are used in the model fitting.

The parameter estimates for model (1) are shown in Table 2. The estimate of the total number of tree species for which the tree diameter is greater than or equal to 10 cm is 376 [approximate 95% confidence interval (367, 386)]. This fitted model has a satisfactory residual plot (Figure 4).

Table 2. Parameter estimates for Pasirmayang for model (1), (d_{min} =10 cm)

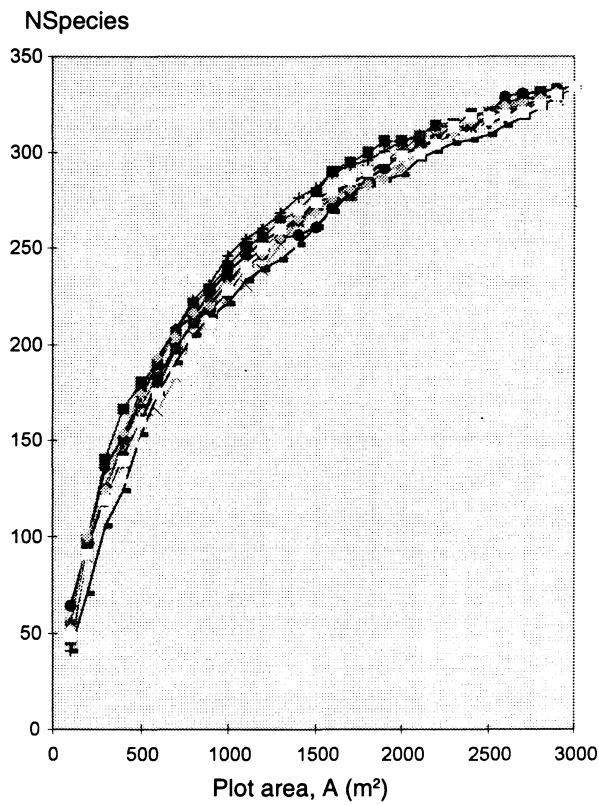| Parameter	Estimate	Asymptotic std. error	Asymptotic 95 % confidence interval	
			Lower	Upper
K1	376.46	4.63	367.35	385.60
K2	0.93	0.03	0.87	0.99
K3	0.74	0.01	0.72	0.77

Figure 3. Pasirmayang: species–area curves for the original and ten random plot re-orderings, (d_{min} = 10 cm)
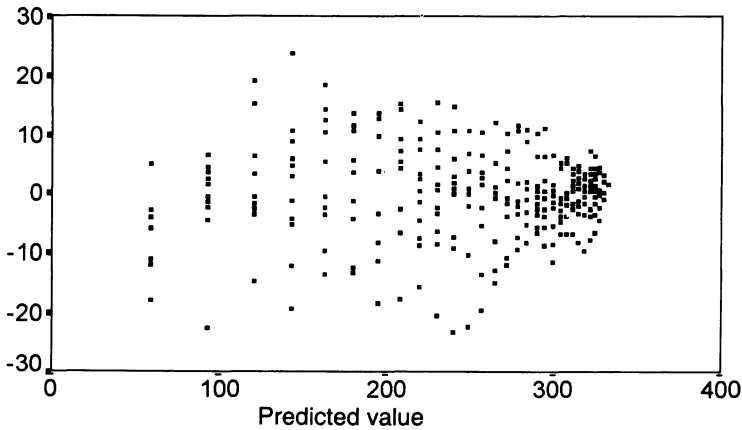

Figure 4. Pasirmayang: residual plot for fitted model, (1), (d_{min} = 10 cm)

Figure 5 shows the species–area curves for the 3-ha plot for trees of diameter greater than, or equal to 3 cm. Fitting model (1) yields the parameter estimates shown in Table 3 with an asymptotic species number estimate of 567 [approximate 95% CI (555, 580)], which may be compared with the estimate of 376 (tree diameter ≥10 cm). Movement from a diameter cut-off of 10 cm to 3 cm results in an estimate of the species carrying capacity which is increased by 51%.
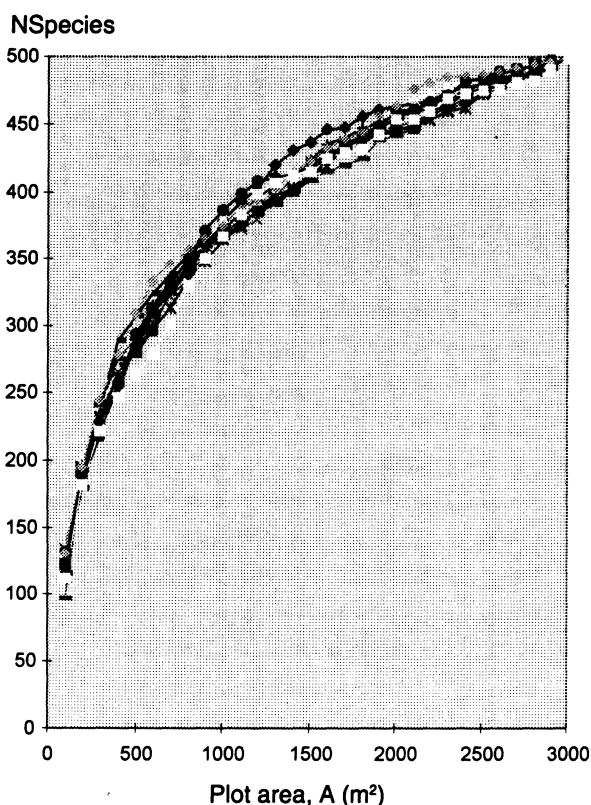

Figure 5. Pasirmayang: species–area curves for the original and ten random plot re-orderings, $(d_{min} = 3$ cm$)$

Table 3. Parameter estimates for Pasirmayang for model (1); $(d_{min} = 3$ cm$)$

Parameter	Estimate	Asymptotic std. error	Asymptotic 95 % confidence interval	
			Lower	Upper
K1	567.81	6.33	555.35	580.27
K2	1.11	0.04	1.03	1.18
K3	0.60	0.01	0.59	0.62

Tebopandak

Species–area data for 11 orderings of the area increment process are shown in Figure 6; one, in which the data were collected, and the plots numbered, and 10 random permutations of the plots sequence. Since the cumulative areas differ for each of the illustrated area curves, only the scatter diagram of all the points on all the curves is presented. The fitted parameters of model (1) to the points on the 11 species–area curves are given in Table 4.
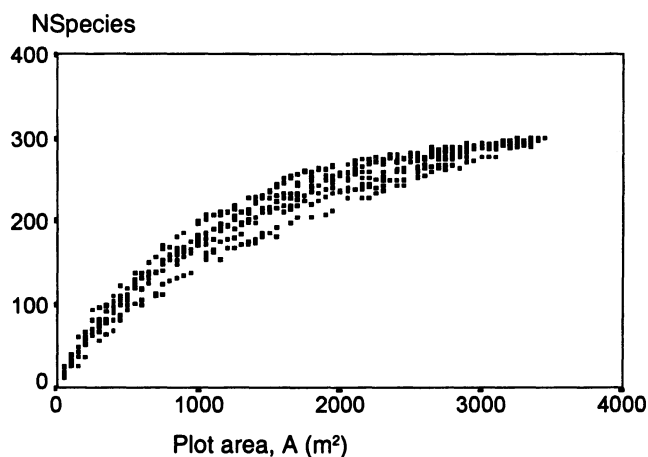

Figure 6. Tebopandak: superimposed species–area curves for 11 plot sequences, $(d_{min} = 10$ cm)

Table 4. Tebopandak: parameter estimates for model (1) ; $(d_{min} = 3$ cm)

Parameter	Estimate	Asymptotic std. error	Asymptotic 95 % confidence interval	
			Lower	Upper
K1	345.33	7.77	330.06	360.60
K2	0.70	0.03	0.65	0.75
K3	0.85	0.02	0.81	0.89

Thus, the estimate of the species carrying capacity (tree diameter ≥ 10cm) is 345 [approximate 95% confidence interval (330, 361)].

Species–diameter curves

The study location at Pasirmayang has been sampled down to a minimal diameter of 3 cm on a 3-ha plot. Figure 7 shows the natural logarithm of the number of observed species (*NSpecies*) plotted against the diameter cut-off, d_{min}, and is a

reasonably linear relationship. This would suggest that a reasonable model of *NSpecies* as a function of d_{min} would be:

$$NSpecies = C1*exp(-C2*d_{min})$$ (2)

Extrapolation to zero diameter cut-off in Figure 7 leads to an intercept of about 6.3, resulting in a rough estimate of the total number of species, for an area of 3 ha, of about 545 [=exp(6.3)].
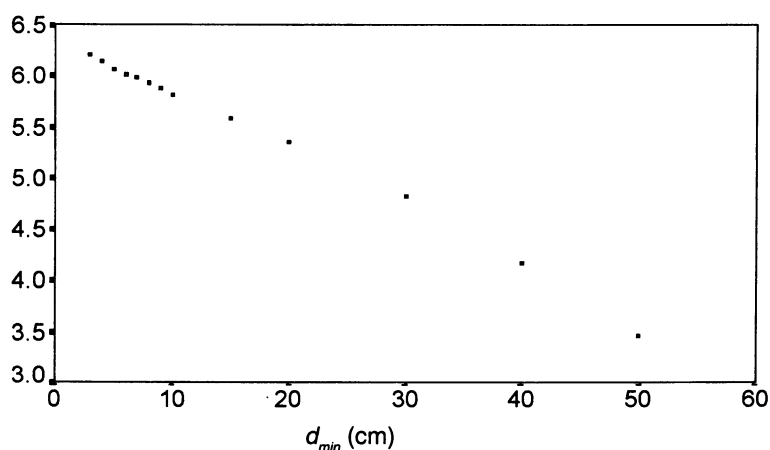

Figure 7. Pasirmayang: plot of log_e (*NSpecies*) as a function of d_{min}

The joint species–area–diameter relationship

How should the empirical species–area relationship, given by model (1), and the empirical species–diameter relationship, given by model (2), be combined into a joint model which adequately summarises the joint variation of the number of species observed with sample area, and diameter cut-off? It is not entirely obvious what the joint form of the model should be. To progress on this, we adopt an entirely empirical approach and examine Figure 8 which shows the relationship between $log_e(NSpecies)$ and d_{min} for the whole plot of 3 ha, and for sub-areas of area 2 ha and 1 ha. It seems that the relationship between $log_e(NSpecies)$ and d_{min} is linear with both intercept and slope depending on area. The three linear trends in Figure 8 may be modelled by :

$$E[log_e(NSpecies)] = \beta_0 + \beta_1 \delta_1 + \beta_2 \delta_2 + \gamma_0 d_{min} + \gamma_1 \delta_1 * d_{min} + \gamma_2 \delta_2 * d_{min}$$ (3)

where δ_1 and δ_2 are dummy variables indicating the sub-areas of area one and two hectares respectively. When model (3) is fitted, using OLS, the parameter estimates given in Table 5 are obtained.
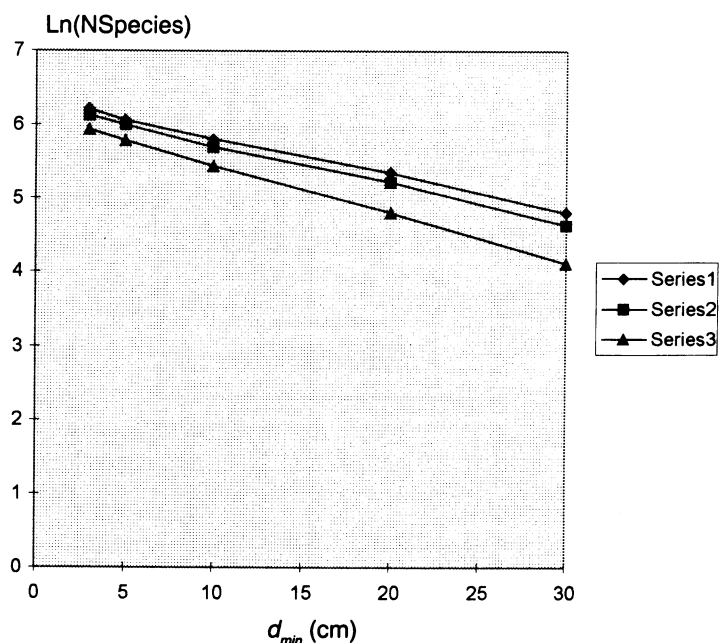
Figure 8. Pasirmayang: relationship between $log_e(NSpecies)$ and d_{min}.
Plot areas: 3 ha (Series 1); 2 ha (Series 2); 1 ha (Series 3)

Table 5. Parameter estimates from fitting model (3) to the data in Figure 8

Variable	B	se B	t	p-value
DUM1	-0.23	0.03	-8.42	0.00
DUM2	-0.08	0.03	-2.89	0.01
DMIN	-0.05	8.E-04	-63.40	0.00
DUM1D	-0.014	0.002	-8.40	0.00
DUM2D	-0.0013	0.0016	-0.78	0.45
(Constant)	6.36	0.014	445.	0.00

The parameter estimates in Table 5 correspond to the following generic linear relation

$$log_e(NSpecies) = intercept(A) + slope(A)*d_{min} \qquad (4)$$

with A taking values of 3, 2 and 1 ha. Using Table 5 we obtain the following fitted linear relations:

$A = 3$ ha: $log_e(NSpecies) = 6.359 - 0.053d_{min}$
$A = 2$ ha : $log_e(NSpecies) = 6.278 - 0.054d_{min}$ (5)
$A = 1$ ha: $log_e(NSpecies) = 6.124 - 0.067d_{min}$

Supposing that the *intercept* in (4) has a maximal asymptotic value as A approaches infinity, the intercept values given in (5) may be described by the relationship:

$$intercept(A) = 5.831 + 0.6177*[1-exp(-0.6425*A)] \qquad (6)$$

If we assume that the diameter distribution of every species is such that for $A = \infty$, the observed diameters of trees will exceed any finite diameter cut-off, then as $A \to \infty$ so will *slope (A)*, in (4), approach zero. The slope values shown in (5) may then be described by the relationship:

$$slope(A) = -0.74*exp(-0.125*A) \qquad (7)$$

Combining relations (4), (6) and (7) leads to the empirical descriptive joint species–area–diameter model:

$$NSpecies = 632*exp \{- 0.6177*exp(- 0.6425A) - 0.74*d_{min}*exp(- 0.125A) \} \qquad (8)$$

It is noted that the form of (8), as a function of A, is different from model (1). A longer sequence of areas in (5) would need to be used in order to fit more complex models than (6) and (7). From (8), as $A \to \infty$, and $d_{min} \to 0$, then *NSpecies* $\to 632$, our best estimate of the total species carrying capacity at Pasirmayang.

Conclusion and discussion

The extended inverted exponential model seems to be well suited to fitting species–area curves. A summary of the parameter estimates for this model (1), for the three study sites, is shown in Table 6.

Table 6. Summary of parameter estimates for model (1)

		K1	K2	K3
Batang Ule	$(d_{min} = 10$ cm)	676	0.523	0.834
Tebopandak	$(d_{min} = 10$ cm)	345	0.700	0.847
Pasirmayang	$(d_{min} = 10$ cm)	376	0.929	0.744
Pasirmayang	$(d_{min} = 3$ cm)	567	1.107	0.604

It can be concluded that the hilly Batang Ule site is substantially more diverse, in terms of the total number of species which could be carried, than both the Pasirmayang and Tebopandak sites. In terms of conservation policy this would mean that rather more emphasis should be put on conserving hilly sites on a granite substratum. However, it has not been established that the Batang Ule diversity space encompasses that of Pasirmayang and Tebopandak. A joint analysis of the data sets would be necessary to establish or refute this.

For the Pasirmayang study site, with tree diameter greater than or equal to 3 cm the asymptotic species number estimate of 567 is considerably higher than the estimate of 376 species, from the data for trees with diameter greater than of equal to 10 cm. The empirical modelling of the joint species–area–diameter relationship leads to an estimated maximal carrying capacity on the Pasirmayang-type forest of about 632 species, 68% larger than the species carrying capacity estimated from simple species–area relationships for trees of diameter greater than or equal to 10 cm in diameter. If the same inflation factor is applied to the Batang Ule site then the estimated total carrying capacity of a very large region like Batang Ule would be 1136 species! Hubbell and Foster (1983) showed that patchy distributions of rare species (a factor not considered in this paper) could cause an underestimation of unobserved species resulting in a total species estimate which is 10-20% too low.

The models used in this paper have been descriptive in nature, being chosen to represent adequately the patterns and relationships in the observed data. It would be much more satisfying if the models used were suggested by a theoretical model of forest structure. Unfortunately there is no adequate model of forest structure available at this time to derive the form of the species–area, species–diameter and species—area–diameter relationships.

The model fitting for the effect of d_{min} has rested largely on the high quality data that has been collected in the Pasirmayang site; all species down to a minimal diameter of 3 cm were identified. However, analysis of data sets collected on larger areas, and to smaller diameter cut-offs than used at Pasirmayang is required. Such data have been collected at a number of sites throughout the world, where the area sampled has been 50 ha, and the diameter cut-off has been 1cm, and subjected to a range of analyses (Ashton 1969, 1976, Appanah & Weinland 1993, Baillie *et al.* 1987, Manokaran & LaFrankie 1990). Unfortunately these data sets do not seem to be publicly available.

Most of the concern in ecological circles, when considering sampling for the assessment of species diversity, is the effect of using a finite sample area on the estimate of the species carrying capacity. It is clear that the diameter cut-off also has a major impact on the estimate of the species carrying capacity. In sampling exercises, the diameter cut-off should not be chosen lightly, and it may be worth adopting field sampling procedures so as to involve some sub-sampling of the primary sample area, where the diameter cut-off is set much lower than in the primary plots.

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