

## **An extreme-value approach to detect clumping and an application to tropical forest gap-mosaic dynamics**

DOUGLAS SHEIL\*<sup>1</sup> and MARK DUCEY†

\**Center for International Forestry Research, P.O. Box 6596, JKPWB, Jakarta 10065, Indonesia*

†*Department of Natural Resources, 215 James Hall, University of New Hampshire, Durham, NH 03824, USA*

*(Accepted 24th September 2001)*

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**ABSTRACT.** Although forest tree pattern-dynamics has long been a focus for ecological theory, many aspects of basic analysis remain problematic. This paper describes, examines and illustrates an ‘extreme-value’ approach to clump detection. Simulations demonstrate that the approach, though simple, is sensitive and well suited to identifying aggregation, even in small data sets. The test is complementary to the  $\chi^2$  approach and significantly outperforms it when high-density clusters form a relatively small fraction of the total area. This difference holds true as density declines, though the power of both tests decreases and the  $\chi^2$  test eventually fails. Though powerful, the extreme-value tests are slightly conservative. The approach is adaptable to other null distributions and applications. An illustration uses tree data from a Ugandan forest plot with records from 1939 to 1992. One plausible explanation for observed stem increases in this plot is an unusually high incidence of large tree-fall events. Evidence for this is sought through spatial localization of various stem populations. Chi-square tests detect non-random density patterns in the populations that comprise ‘all stems  $\geq 10$  cm diameter recorded in the 1992 survey’, and ‘all recruits in 1976’. In the extreme-value test three populations are found to be clumped, these are ‘pioneers  $\geq 10$  cm diameter recorded in the 1992 survey’, ‘all recruits in 1992’ and again ‘all recruits in 1976’. These patterns, particularly the pioneer trees and stem recruitment, signal a ‘gap-dynamic process’ of tree regeneration. Despite this, the trends observed in the Ugandan plot appear unlikely to be caused by tree-falls alone. Various technical and ecological aspects of the extreme-value approach and tree spatial analyses are discussed.

**KEY WORDS:** aggregation, asymptotic distribution, pattern analysis, permanent sample-plot, African rain forest, Uganda

<sup>1</sup> Corresponding author.

## INTRODUCTION

It has long been asserted that forests exhibit 'gap-mosaic' stem-dynamics (Armesto *et al.* 1986, Aubréville 1938, Newbery *et al.* 1986, Oldeman 1990, Pickett 1980, Watt 1947, Whitmore 1982). Such concepts have been influential in forest ecology, and have even been elaborated as explanations of tropical forest richness (Brandani *et al.* 1988, Brokaw 1987, Brown *et al.* 1999, Denslow 1987). Despite this, the quantified evaluation of tropical forest tree distributions remains poorly developed (Clark & Clark 1984, Lieberman & Lieberman 1994). There have been advances in the spatial analyses of individual species in large short-term study plots (Hubbell *et al.* 1999, Welden *et al.* 1991) but few developments pertain to stand-level processes (Pélissier 1998). Evaluations of longer-term pattern dynamics remain especially rare (Lieberman & Lieberman 1994; but see Lieberman *et al.* 1985, Sarukhán *et al.* 1985).

This paper presents an extreme-value approach to detect stem clumping. The method addresses the question 'what is the probability, under the null-hypothesis, that the most densely stocked cell will have a count as high as that recorded?'. This proves to be simple to implement and powerful. Problematic assumptions need not be as troubling as they initially appear. Cressie (1993, p. 590) for example, considers that it is good practice to detect departure from randomness prior to further analyses of point patterns. While spatial autocorrelation (cf. Legendre 1993) is ignored in our formulation, detecting such non-random effects is the key step in the investigation.

Statistical assessments of spatial distributions however require several basic considerations: the nature of the null-hypothesis, the scale of assessment, the 'type' of deviation that is to be distinguished, and the underlying assumptions. Each is examined further below, where in particular we use simulations to compare and quantify the statistical properties of the extreme-value and  $\chi^2$  tests. First, however, in order to elaborate the ecological relevance of these concepts, we shall introduce the field data with which we explore and illustrate the approach.

## THE DATA

*A plot in Uganda*

Our study focuses on plot 7 of Eggeling (1947), a 1.86-ha plot first measured in 1939 and situated in Budongo, Uganda, 1°37'–2°03'N and 31°22'–46'E (Eggeling 1947, Sheil 1998, Sheil *et al.* 2000). This is an area of mixed deciduous rain forest on ancient red-clay soils at an altitude of *c.* 1000 m asl, and with an annual rainfall *c.* 1500 mm  $y^{-1}$ . The plot is located in mature pristine vegetation on level well-drained ground. The canopy includes a high proportion of *Cynometra alexandri* C. H. Wright (Caesalpiniaceae), a buttressed species that can reach to over 50 m tall. This species can form near-monodominant stands which are generally viewed as the local climax vegetation (Eggeling 1947). In 1992 a

census recorded the location of all tree stems over 10 cm diameter at reference height (drh, usually 1.3 m, but higher on buttressed or deformed stems, see Sheil 1995, 1998). Accuracy was good with over 75% of stems being recorded within 0.3 m and 95% within 1.5 m of previous records on 'blind' re-measurement ( $n = 573$  based on a 20% check of this and four other plots, Sheil 1995, 1996a). This plot is believed to be the oldest surviving study plot in mature pristine forest anywhere in the tropics.

As all stems are individually labelled, the 1992 tree locations can be used to assess past recruitment patterns within this population. As the minimum stem sizes recorded have varied with recording dates, there are choices as to how to handle recruitment data. The data used here draw on the 1939, 1952, 1976 and 1992 assessments. While a minimum stem size of 20 cm drh can be applied generally, it greatly reduces the number of observations available from those censuses where many smaller stem records are available.

This plot has previously revealed some unexpected trends (Sheil 1998, 2001; Sheil *et al.* 2000). There is a substantial (*c.* 25%) long-term increase in the stem density (from  $472 \text{ ha}^{-1} \geq 10 \text{ cm dbh}$  in 1939 to  $586 \text{ ha}^{-1}$  in 1992). An increase was also recorded in four other, but not pristine, long-term plots (Sheil 2001). Various explanations can be proposed. By developing associated predictions, these can in turn provide testable hypotheses. One plausible explanation is that the changes are merely chance fluctuations due to large tree-falls. Analyses of plot 7 have already determined that most basal area losses over the period of observation occurred through the loss of a very small number of large stems more than a metre in diameter. Specifically the death of only seven stems contributed over 60% of the net stem basal area losses recorded over the 53-y period of observation (Sheil *et al.* 2000).

In developing our 'tree-fall explanation' into a testable hypothesis, we explicitly predict that the increase in stem numbers will be spatially associated with the open sites left by the loss of a few large stems. The canopy in this forest type is tall and closed, the understorey is shaded, and pioneer species are rare. It is implicit in our tests that in such an environment, tree-falls can greatly increase understorey light levels and that these changes are localized. We thus predict that new recruits, especially those of the least shade-tolerant species, will be aggregated. Looking over a stem-map (plot 7, individuals  $\geq 10 \text{ cm}$  diameter in 1992, D. Sheil unpubl. data) clumps seem apparent, but the human eye is notorious for seeing such structure in randomness. The challenge is to provide an *objective* assessment.

#### *Analysis of the plot data*

The evaluations are based on tabulating defined tree populations over each of 80 square *c.* 15-m-sided (actually 50 feet) grid-cells (i.e.  $\approx 225 \text{ m}^2$ ) allocated  $10 \times 8$  over the *c.*  $150 \times 120\text{-m}$  ( $500 \times 400$  feet) plot. This scale relates to the size of 'gaps' seen from large tree-falls (a 1-m-diameter tree has a *c.* 15-m-wide

canopy). There is another more practical reason: the whole plot has been measured by crews who have, on some occasions, cut an accurate grid ( $5 \times 4$ ) of access lines through the understorey – the quartering of these major grid-squares to provide our grid-cells means that two edges, no more or less, of each lie on the cut-lines and any impact on regeneration is thus equivalent.

Stems were classified according to various criteria, including size, recruitment period and guild (following Hawthorne (1996), see the footnote 6 of Table 1 for a brief description, and Sheil *et al.* 2000 for a full species-to-guild listing). Cell-counts for each were tabulated by frequency. Populations were chosen to reflect the emphasis on tree-fall gaps and young forest regrowth, e.g. small trees, pioneer species, and the temporally distinct patterns of recruitment available in the long-term data. For comparison and to inform later interpretation the distributions of other populations are included. It is not appropriate to make Bonferroni corrections to these probabilities as some populations overlap, and the range of tests and populations are being made for the sake of comparison and illustration. They are neither equal nor independent with regard to the main hypothesis.

The null hypothesis assumes a homogeneous Poisson distribution, which is the technical way of saying an unbiased random and independent placement of stems. Two types of analyses are applied to each population against this null hypothesis. In the first a  $\chi^2$  test of the actual-versus-expected distribution was undertaken using *StatGraphics Plus* (1993), which automatically groups and tabulates frequencies so that all expected counts are at least 4 and adjusts degrees of freedom accordingly. The second approach was to identify the highest cell-count (most extreme value) for each population and assess the probability that this would be observed under the null hypothesis. For such an assessment of presumed low probability events in a pre-defined population, a ‘tail-end approximation’ is appropriate (Hanley & MacGibbon 1995) and is undertaken here by calculating the one-cell probability,  $P_1$ , and what we shall call the  $P_{80}$  ‘80-cell probability’ (or  $P_n$  where  $n = 80$ ). Hanley & MacGibbon (1995) propose  $P_n = 1 - \exp(-nP_1)$  which is the form we use (but see discussion).

The one-cell ( $P_1$ ) probability value that we use is one minus the area under the Poisson distribution from zero up to one less than the maximum cell count,  $M$ , i.e.

$$P = 1 - \sum_{k=0}^{M-1} \frac{e^{-\lambda} \lambda^k}{k!} \quad (1)$$

where  $\lambda$  is the mean per-cell stem density from the whole plot. This was calculated using standard MS-Excel functions. In all cases, the actual and expected distributions were also examined graphically. No correction is made for the one degree of freedom lost in assessing the mean stem density, which may raise concerns about inflated P values – though as we shall show below these concerns are unfounded.

Technically a binomial formulation could be an appropriate means to test the cell-count distribution given the defined total counts. Both approaches have been evaluated and, as might be expected, the results generated with binomial and Poisson distributions proved almost identical. The binomial evaluations proved very fractionally less conservative, and will not be presented separately here.

#### *Tests of power and Type I error rate*

Whenever a new procedure is proposed, it is instructive to examine the power of the test, and to verify that its error rate under the null hypothesis is correct. The power of a test is defined as the probability, given a specified degree of departure from the null hypothesis, that the test will actually return a significant result (Toft & Shea 1983). In other words, power is the probability of rejecting the null, when the null is actually false (i.e. power = 1 – Type II error rate, here when  $\alpha = 0.05$ ). A related quantity is the Type I error rate, defined as the probability of rejecting the null hypothesis when the null hypothesis is actually true. In principle, this probability should equal the  $\alpha$  chosen for the test. So, for example, when we select  $\alpha = 0.05$ , we should falsely reject the null 5% of the time even when it is true.

We tested the power and Type I error rate of the extreme-value test, in comparison to the  $\chi^2$  test, using a Monte Carlo approach. We assumed the forest was composed of two types of areas with two different densities, a background density of mature forest, and a higher density corresponding to regenerating gaps. Within each type, we assumed the forest was a random ‘Poisson forest’. In statistical parlance, we used a finite mixture model of two distributions, each being Poisson. By varying the proportion of the two distributions, and the density corresponding to each distribution, we were able to simulate a range of forest structures. We tested three density combinations: (a) background density of 10 individuals per cell, and high density of 20 individuals per cell; (b) background density of 2 individuals per cell, and high density of 4 individuals per cell; and (c) background density of 0.4 individuals per cell, and high density of 0.8 individuals per cell. These density combinations approximate the range for the populations examined in the Ugandan data.

For each iteration we simulated 80 cells. Each cell was randomly assigned to the background type or the regenerating type, with probability according to the mixture being simulated. The density of that cell was taken from the Poisson distribution corresponding to the density of the type. Once values were established for all 80 cells, the extreme-value test and the  $\chi^2$  test were performed on the simulated data, using the simulated data to provide the estimate of overall density. For the  $\chi^2$  test, the data were adaptively binned using that simulated data to yield expected values of at least four cells in each bin. A test was scored as significant for each test using an  $\alpha$  of 0.05. We performed 10 000 iterations at each combination of mixture proportion and density for the simulations.

## RESULTS

*Forest data*

The full summary of results for the populations examined is provided in Table 1. The  $\chi^2$  test indicated that only two populations had significantly non-random stem density distribution. These were 'all stems in 1992' and 'all stems first recorded in 1976'. The observed and null stem-frequency distributions for these two larger populations are shown in Figure 1. Three populations are significant in the extreme-value test, these are the pioneers, 'all new stems in 1976', and 'all new stems in 1992'.

*Simulation tests*

The results of the simulated power and error rates are shown in Figure 2. Both tests show considerable power when expected densities are high, though in different regions of the mixture frequency. The  $\chi^2$  test is more powerful when the frequency of background and high-density cells is approximately

Table 1. Evaluations of cell occupancy by various stem populations in plot 7 Budongo (1992 tree positions map), in relation to a null hypothesis of a random (Poisson) distribution.

Stems selected	----- $\chi^2$ test -----				----- Extreme value test -----		
	Mean cell count <sup>1</sup>	$\chi^2$	df	P	Max. count	Poisson cell <sup>2</sup> P <sub>1</sub>	Poisson all <sup>3</sup> P <sub>80</sub>
$\geq 10$ cm dbh <sup>4</sup>	13.60	14.1	6	0.028*	25	0.0036	0.250
$\geq 20$ cm dbh <sup>4</sup>	4.30	2.37	6	0.88	10	0.014	0.674
$\geq 50$ cm dbh <sup>4</sup>	0.76	0.03	1	0.84	3	0.044	0.970
10–20 cm dbh <sup>4</sup>	9.25	4.04	7	0.77	17	0.014	0.674
20–30 cm dbh <sup>4</sup>	2.61	4.66	4	0.32	7	0.018	0.763
10–30 cm dbh Non-pioneer light demanders <sup>4,5</sup>	1.43	2.55	2	0.28	6	0.0065	0.405
10–30 cm dbh Shade bearers <sup>4,5</sup>	10.12	4.63	6	0.59	20	0.0067	0.415
10–30 cm dbh Pioneers <sup>4,5</sup>	0.35	–	–	–	4	0.00047	0.037
New 1939, $\geq 15$ cm dbh <sup>4,6</sup>	1.92	4.69	3	0.20	6	0.014	0.674
New 1952, $\geq 15.4$ cm dbh	0.82	0.22	1	0.64	3	0.051	0.983
New 1976, $\geq 8.7$ cm dbh	8.08	12.0	6	0.05	20	0.00029	0.023
New 1992, $\geq 10$ cm dbh	2.70	0.86	4	0.93	11	0.00016	0.013
New 1939, $\geq 20$ cm dbh	1.85	1.63	3	0.65	6	0.011	0.585
New 1952, $\geq 20$ cm dbh	0.48	0.36	1	0.55	2	0.082	0.999
New 1976, $\geq 20$ cm dbh	1.00	0.95	2	0.62	4	0.019	0.781
New 1992, $\geq 20$ cm dbh	1.16	1.16	2	0.50	3	0.11	1.000

<sup>1</sup>The total number of stems is this figure multiplied by 80.

<sup>2</sup>The value given is the probability of the highest count arising by chance in any one cell.

<sup>3</sup>This value,  $P_{80} = 1 - \exp(-80 \times P_1)$ , is the estimated probability of this highest cell density given the total number of cells observed (Hanley & MacGibbon 1995), alternative forms are discussed in the main text.

<sup>4</sup>Based on all stems recorded in 1992, (n.b. there are no multiple stemmed individuals).

<sup>5</sup>Guild classes follow those detailed by Hawthorne (1996), see Sheil *et al.* (2000) for a full species-to-guild listing. The system is based on juvenile and adult prevalence in both well-illuminated and shaded conditions. To avoid circularity the species were classed without reference to the Budongo plot data. In brief: Pioneer seedlings and adults are found almost exclusively in well-illuminated areas. In contrast seedlings and adult shade bearers are found in shaded (gap free) forest. While the seedlings of non-pioneer light demanders can persist in shade they require good light for growth and development.

<sup>6</sup>Note that these are not true recruits – but 1992's survivors from the first census.

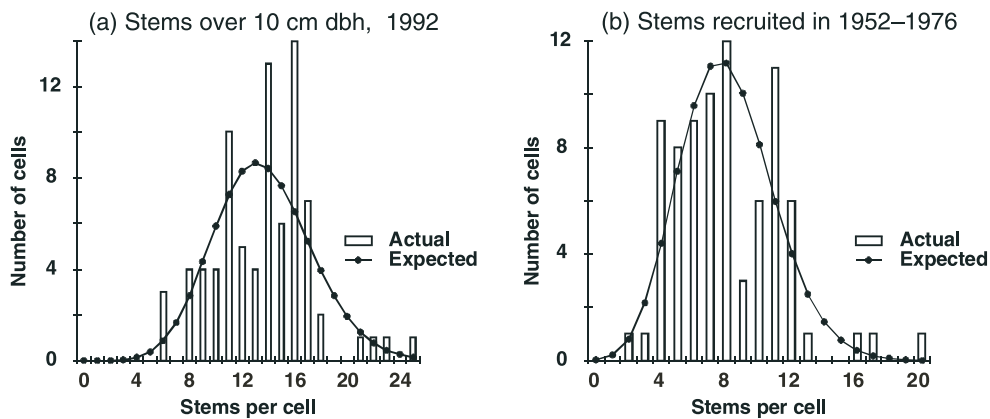


Figure 1. Stem density distribution for two populations in 80 c. 15-m x 15-m (actually 50 feet) grid squares, or cells, for plot 7 Budongo, using tree-map data produced in 1992. (a) All stems  $\geq$  10 cm dbh in 1992; (b) Stems recruited to 10 cm dbh and over between 1952 and 1976. The ‘expected’ curve is calculated assuming a homogeneous Poisson distribution. Note the high-density outliers on the right of each distribution.

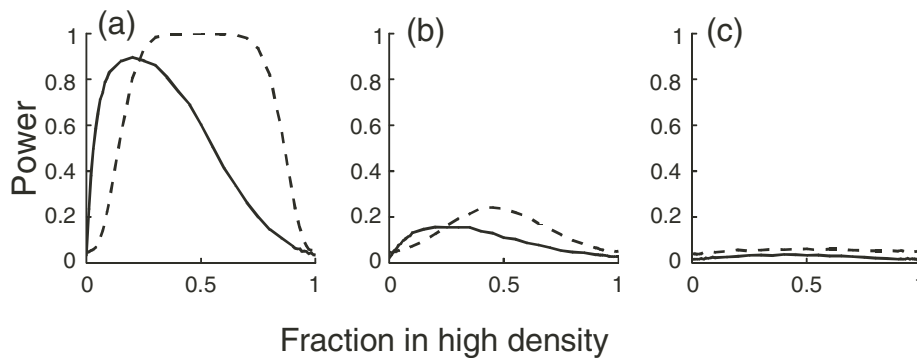


Figure 2. Power comparison of  $\chi^2$  (dotted-line) and extreme-value (full-line) tests for three density combinations: (a) background density of 10 individuals per cell, and high density of 20 individuals per cell; (b) background density of 2 individuals per cell, and high density of 4 individuals per cell; and (c) background density of 0.4 individuals per cell, and high density of 0.8 individuals per cell.

equal. By contrast, the extreme-value test is more powerful when high-density cells form a relatively small fraction of the total, i.e. ‘clumps’. This pattern holds true as density declines, though the power of both tests decreases. Eventually when data are so sparse that the power of both tests is low, the  $\chi^2$  test has marginally higher power (Figure 2c). In this range, the  $\chi^2$  approach is sometimes inapplicable due to inadequate counts, and the power difference has little practical relevance as neither method has appreciable power in such circumstances.

The Type I error rate of the two tests is also informative. The  $\chi^2$  test is not significantly different from alpha in its Type I error rate, except at the lowest density under the null hypothesis (0.4 individuals per cell), where the Type I

error rate fell to 0.039. At this density as already noted the  $\chi^2$  test occasionally fails because of inadequate observations. The extreme-value test is more conservative than the nominal alpha across the entire range of densities, with actual error rates of 0.034 at the highest density (20 individuals per cell), ranging smoothly down to an error rate of 0.016 at the lowest density.

#### DISCUSSION

##### *Forest data*

All but one of the significant results occur in populations expected to respond to canopy gaps. The remaining case, the entire undifferentiated stem-population (all-stems 10 cm and over) has the largest population size examined. Any conclusion of a general 'non-random pattern' is not supported when arbitrary subsets such as the 10–20 cm and 20–30 cm populations are examined, and indeed 'high-per-cell clumping' is not seen in either these or the full population by the extreme-value method. Only in the case of the 1976 recruits do both analyses yield a significant result – this is again for a large population with over 640 stems, but this time density observed in the densest cell (Figure 1b) denotes clumping. The other two significant results are revealed only by the extreme-value procedure.

Given the detection of clumping in the 1976 recruits a clearer pattern for a more recent period would be predicted if gap processes are indeed responsible. This is indeed seen by the extreme-value tests as the 'All stems recorded for the first time in 1992' population gives the most significant result ( $P = 0.013$ ) even though the population is less than a third of that involved in the previous period and significance is not revealed by the  $\chi^2$  test. The oldest 'true regeneration' (the 1952 population) gives no indication of aggregation.

The extreme-value approach also indicates a clump in the small population of pioneer stems (10–30 cm dbh). In this case, the  $\chi^2$  test could not even be applied, as the stem numbers are insufficient. The detection of clumps cannot attribute causes. Other explanations are possible: vegetative regeneration, seed-fall patterns, intra-tree below-ground interactions and other more exotic ideas may be reasonable alternatives, and indeed all these could be sought out in an equivalent fashion using the extreme-value approach. However, the fact that clumping is seen in a tiny population of pioneer species strongly indicates illumination as a major factor.

##### *Power, error rates and more exact approximations*

The difference in sensitivity of the two tests, as clearly seen in Figure 2, indicates that they are complementary. The difference between the extreme-value and a  $\chi^2$  approach is that the former focuses only on the extreme tail-end deviation, while the latter examines the overall distribution. The extreme-value approach clearly outperforms the  $\chi^2$  when applied to localized and discrete clumping. Not only that, but the test remains conservative. This conservativeness appears to arise from the use of the observed density, rather than

the ‘true’ density of the population, in performing the test. Consider, in a population that obeys the null hypothesis, drawing a sample of cells that includes an extremely high-density cell purely by chance. Now, when the density is calculated from the sample, that high-density cell is factored in, leading on average to an inflated estimate of the population density. Then the sample density is used to test whether the high-density cell could have arisen by chance. But because the sample density is (on average) high, the probability corresponding to the observed extreme density will be (on average) over-estimated as well. This leads to inherent conservatism in the test, and it may fail to detect real patterns. On the other hand, when the test does return a significant P-value, we can be confident that the correct probability is at least as low as indicated by the test.

At very low densities, such as those depicted in Figure 2c, the  $\chi^2$  test does slightly outperform the extreme-value approach. However, performance at these density ranges are largely irrelevant, since neither method has more than a trivial chance to return a significant result, even when the null hypothesis has been seriously violated. Under these conditions the  $\chi^2$  test often fails altogether as sufficient counts are not recorded. At such densities many observations consist of empty cells or of cells with one, or possibly two, tallies. Attempts to detect non-randomness by examination of cell counts alone, when those counts represent a meagre sample of sparsely distributed individuals, can only prove frustrating. In such cases, tests that use inter-tree distances or other additional information will likely be required to detect non-random distributions.

We have followed the procedures of Hanley & MacGibbon (1995) to calculate the aggregated probability values ( $P_n$ ). But two other approaches should be recognized. The simplest approximation is  $P_n = P_1 \times n$ . Despite not being a ‘true’ P-value (it is not bounded between zero and one), it tends conservatively towards the true answer as the  $P_n$  values get small enough to be significant: i.e. using 80 cells ( $P_n = P_1 \times 80$ ) results in differences  $< 1\%$  in  $P_{80}$  for all significant values.

An alternate and fully correct procedure is available under the assumption of our null hypothesis that the abundances on all the plots are *independent*, so the probability that a plot has  $\geq n$  individuals is independent of the abundances on the other plots. If there are  $n$  plots, and  $P_1$  is the single-plot P-value calculated using equation 1, then the probability level assuming  $n$  independent plots ( $P_n$ ) is

$$P_n = 1 - (1 - P_1)^n$$

This is derived as follows:  $(1 - P)$  is the probability that a single plot contains  $< M$  individuals under the null hypothesis. The probability that all  $n$  plots contain  $< M$  individuals under the null hypothesis is  $(1 - P)^n$ , which is the same as saying that no plots contain  $M$  or more individuals. The converse proposition is that at least one of the  $n$  plots contains  $M$  or more individuals.

Since ‘no plots  $\geq M$ ’ and ‘1 or more plots  $\geq M$ ’ are mutually exclusive and exhaustive, the probability that at least one plot contains  $M$  or more individuals, under the null hypothesis, is  $1 - (1 - P)^n$ . This alternate formula again gives results that are for all practical purposes identical to the Hanley & MacGibbon (1995) formula. For our results, all three approaches, using 80 cells, result in negligible differences to any significant probability values. However, our more precise power version as above should be considered if accurate higher  $P_n$  values are of interest, e.g. for meta-analyses.

We have not examined other approaches to evaluating spatial pattern but some brief comments on the Kolmogorov–Smirnov (K–S) approach are relevant as, after the  $\chi^2$  method, this is probably the most conventional approach. The extreme-value and K–S approaches are unrelated. The K–S test is most sensitive to deviations from the null hypothesis found close to the median value of the distribution while the extreme-value test addresses the (upper) tail. The K–S approach would be most useful if there were a very large number of plots and deviations being sought in the middle range. Again, the extreme-value method will be more suitable when clumping is sought, especially if the number of plots is small.

Our examples are specific, but the concepts and advantages behind the extreme-value approach are general. The approach can be applied to other null distributions and applications and yield similar advantages to those we have investigated, namely high power with detecting anomalously high frequencies in modest data sets. Other adaptations are also possible, for example, as long as per-cell probabilities are sufficiently low the analytical arguments could be easily re-defined to find anomalously low frequency counts or ‘holes’ in high-density distributions.

#### *Meaningful assumptions?*

A review of choices and assumptions is a prerequisite to interpreting results further. A random distribution is a naïve null hypothesis – why should trees be randomly distributed? Various factors influence any spatial distribution; it is this process-dependent pattern, minus an increase in canopy-gap-mosaic aspects, that ought to serve as our comparison. However, just what this *realistic* null distribution should be is unclear. The scale of pattern anticipated for individual tree-falls defines our scale of assessments. However, these large trees reach to over 50 m, and the increase in light following their death will thus have some influence over potentially much larger areas – an aspect that is accessible to further field-based investigation. Here, we consider the more general and conceptual aspects of what our tests mean.

A probability threshold ( $P \leq 0.05$ ) has been used to ‘detect’ deviations from random. Despite theoretical debate (e.g. Berger & Selke 1987), this convention provides a useful criterion. We need to remain acutely aware that P-values depend on more than the underlying pattern, being determined also by the amount of data, and the power of the test. The objective way to interpret the

analyses presented here is simply that ‘something unlikely to be random has been detected’. Failure to detect such deviations cannot prove the null hypothesis is true, though through our power analyses we could perhaps have attempted to estimate the upper limit on any such aggregation. Formally, we have assumed that cell densities are independent; though we know this must be untrue (Legendre 1993). As long as this is recognized the test and the definition of clumping it provides remain useful. Autocorrelation actually appears to have little evident effect on local stem pattern given the flat terrain and homogeneous soils of the plot. Any vegetation-based spatial effects are potentially what we are looking to detect so a null hypothesis that denies them is reasonable, but only as a first step (Cressie 1993).

The original question sought an explanation of increased stem recruitment based on the assumption that recruitment opportunities had been *higher than normal* due to tree-fall gaps. We did not however, manage to determine that there would be no spatial clumping in a system where this was not the case. We require a comparison of the patterns and intensities of gap formation: *normal* versus *observed* – but this comparative information is not available. Detecting that gap-patterns do exist is nonetheless helpful in deciding if and how to proceed.

Despite the ecological naivety of a random null model, and the suggestion that it is used principally for exploratory study (Cressie 1993), it remains the basic reference for investigations of stem distribution (Condit *et al.* 2000, He *et al.* 1997). Emphasis on non-random patterns in species has distracted attention from explaining why near randomness is commonly observed at the stand level. Are patterns in fact more random than might be predicted from current understanding? We remain poorly equipped to address such questions, but it is important to assess what facts, or even speculations, might be mustered towards a better understanding.

Though forest regeneration is generally scattered, the underlying seed dispersal distributions are far from random (Nathan & Muller-Landau 2000). Empirical evidence continues to show that while most species are clumped when viewed at a large enough scale *local* patterns are hard to distinguish from random (Dawkins 1952, 1985; He *et al.* 1997; Lieberman & Lieberman 1994; Pires *et al.* 1953). There are also mathematical aspects that may help explain why these mixed populations show near random distributions. For example, under the equivalence theorem the superposition of any two or more Poisson distributions is itself indistinguishable from a single Poisson distribution (Cressie 1993), i.e. if we combine [near] random species distributions they will give overall [near] random stem distributions. Lottery models of species co-existence have been gaining increasing theoretical and field support (Chesson & Warner 1981, Hubbell 1979, Sykes *et al.* 1994). At the whole-stand level, if all species can potentially occupy any site, and the outcome of competition is ‘close to’ random, then canopy space is likely to be the main determinant

of local density patterns, and there are few reasons, other than gap processes associated with massive tree falls, to expect major fluctuations in stem densities within mixed-species communities.

Given that stems are 'locally near-random' our attention then needs to focus on the non-random gradients in density found in all species when viewed across landscapes. To maintain a random stem pattern any non-random density trend in one species needs to be paralleled by an opposite trend amongst others. What are these forces? Certainly stem densities are remarkably consistent across a great range of forest types apparently determined more by canopy packing and physiological size limits than by local conditions (Enquist & Niklas 2001). Such general principles seem to maintain the homogeneity of the general stem densities (Kohyama *et al.* 2001). But at the same time these packing limits appear to falsify a truly random null hypothesis as physical packing limits restrain the number of stems that can be co-located in one space; the Poisson distribution has no such limit.

Can such a disjointed understanding be advanced into deeper ecological insight? Some progress may prove possible by simple process-based pattern assessments (Moravie *et al.* 1997, Ripley 1977), and through tests based on permutation methods (Besag & Diggle 1977, Lieberman & Lieberman 1994, Wills *et al.* 1997). The main challenge however appears to be in finding better null models. One option is to examine different tree 'packing assumptions' as related to different measures of tree basal area, crown area, and size-related 'zone of influence' and determine the sample distributions that arise. Current forest simulators tend to treat space in a very crude and grainy way, but this is adequate for a cell-based analysis. Deeper understanding and predictive power should become accessible through community simulations that implicitly reflect the known behaviour of forest stands (Chave 2001, Hubbell 2001, Sheil 1999). These are the null models we seek.

Forest ecology requires attention on value distributions and spatial arrangements and their transformation over time, rather than simple correlations amongst mean measures or other univariate data (e.g. Sheil 1996*b*). These value distributions and their spatial flux describe the dynamics of forest heterogeneity. This heterogeneity-dynamic governs many processes including those likely to underlie the persistence of species and changes in community richness. In a more applied context, it is fundamental to a better understanding of the effects of interventions and environmental changes to look at how underlying value distributions, and their dynamics, are altered (Cannon *et al.* 1994). This requires the development of suitable assessment methods.

#### *Stem dynamics in Budongo*

The analytical evidence for clumping in plot 7 remains subtle. Are we closer to understanding if tree-falls might explain the increase in stem densities? The spatial analyses do not stand alone. The canopy-opening hypothesis can be

elaborated to suggest additional predictions that can be assessed against the available data.

- (1) A reduction in basal area. The measured basal area in the plot has remained over  $50 \text{ m}^2 \text{ ha}^{-1}$  (Sheil *et al.* 2000). This is a high value and implies the maintenance of dense tree cover.
- (2) Increased tree growth in the residual stems. No general trend is evident in per-stem growth or stand-level basal-area growth, although there was a temporary increase in the p95 (95 percentile) fastest-diameter-growth stems in the period covering 1950 (Sheil 1997).
- (3) Increased recruitment of less shade-tolerant species. An increase in the total number of pioneer stems is found but in relative terms pioneers decrease as the shade-tolerant stems have consistently increased faster (Sheil *et al.* 2000).

In summary, the overall basal area remains high and the understorey is dense. The small numbers of pioneer stems are not sufficient to explain these more general changes. The loss of large trees is a normal backdrop to forest processes and change. The rise in stem number appears more than a local fluctuation and other possible causes merit examination. It may be due to the loss of large ground-dwelling forest fauna: since the eradication of elephants (*Loxodonta africana*) in the 1960s, a major cause of understorey damage and tree mortality has been removed (Laws *et al.* 1975, Sheil 1998).

#### CONCLUSIONS

The extreme-values approach is a powerful and appropriate means to detect clumping, even in small data sets, and merits wider application. The test is complementary to the  $\chi^2$  approach and significantly outperforms it when clumping is sought, i.e. when high-density cells form a relatively small fraction of the total. By contrast, the  $\chi^2$  test is most effective when the frequency of background and high-density cells is approximately equal. Unlike the  $\chi^2$  test, which requires minimum counts in each histogram cell, there are no limiting conditions for the extreme-value test. The test will by definition also outperform the K–S approach in detecting clumping. The extreme-values approach is marginally conservative allowing significant P-values to be viewed with confidence. The extreme-value approach is easily adapted to other null distributions and applications where it can offer similar advantages to those we have identified.

Spatial pattern is detected in the stem dynamics of the Ugandan plot. Chi-square tests show non-random density patterns in the populations that comprise ‘all stems  $\geq 10$  cm diameter recorded in the 1992 survey’, and ‘all recruits in 1976’. In the extreme-value test three populations are found to be clumped: ‘pioneers  $\geq 10$  cm diameter recorded in the 1992 survey’, ‘all recruits in 1992’ and ‘all recruits in 1976’. These results validate a gap-dynamic process of tree regeneration. However, the pattern is slight and it is doubtful that the observed

increase in stem density is caused by tree-falls alone, and other explanations should be sought.

More ecological insight requires the development of more realistic null-hypotheses or comparisons, and on assessing the form of any deviations as opposed to merely detecting them. Nevertheless, the extreme-value approach offers a simple and flexible method for pattern detection.

#### ACKNOWLEDGEMENTS

DS's original study in Budongo was funded by the Overseas Development Administration (now DFID) as project R4737 under the Forestry Research Programme component of the Renewable Natural Resources Research Strategy, while he worked at the Oxford Forestry Institute. A comprehensive list of acknowledgements for the field study is provided in Sheil (1998). William Hawthorne generously supervised the classification of Budongo's tree species to guild types. The New Hampshire Agricultural Experiment Station provided additional support to MD. We are grateful for comments on drafts and related texts by David Newbery, Robert Whittaker, Robert Nasi, Unna Chokkalingam, Jérôme Chave, Ian Turner and reviewers, and for help from Kim (Meilinda Wan) in preparing the text.

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