

Analysing disturbance with the Ewens/Caswell neutral model: theoretical review and practical assessment

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ABSTRACT: The neutral model proposed by Caswell (1976) is discussed and a justification provided for its use in the analysis of ecological disturbance, both physical and biological. Although the Ewens/Caswell neutral model is a powerful analytical tool, in practice it presents serious computational problems which cannot effectively be overcome by subsampling. But attempts to duplicate the effect of the model with simpler equitability methods were unsuccessful.

INTRODUCTION

Science, as Redfield (1958) remarked 'is the construction of models of nature'. Indeed, Hedgpeth (1977) noted that 'marine ecology began with a model... based on observations of the oyster banks of Schleswig-Holstein' (Moebius 1883). We have been experimenting with a neutral model in the field of environmental disturbance, the Ewens/Caswell neutral model, with particular emphasis on the marine environment. In an earlier publication we presented some practical results of this form of analysis (Platt & Lamshead 1985) but left unanswered some of the theoretical questions upon which our use of the methodology rested. Specifically, we deferred comment on 'whether certain models are truly neutral', the 'major problems with attempting to artificially reduce data', 'how the V -statistic compares as a diversity or equitability measure with other approaches in order to justify the investment in computer time' and the question of 'the neutral model being relatively sample size independent' (Platt & Lamshead 1985). In this paper we return to these points and, in addition, consider the following: (1) Why are neutral models useful ecological tools? (2) Why the Ewens/Caswell model?

It seems logical to proceed by considering neutral models in general, the Ewens/Caswell neutral model in particular, the question of its neutrality, its suitability as a disturbance indicator, practical difficulties with obtaining appropriate raw data and finally whether there are any simpler alternative techniques which can achieve similar results without the computational problems associated with this model.

We intend to concentrate once again on disturbance. For, as Price (1984) pointed out, community organization paradigms based on interspecific competition are commonplace 'while the real part that disturbance plays is seldom evaluated'. As in previous papers we define disturbance as 'the process which occurs when any physical or biological agent acts to reduce population size, either by a direct biocidal action or by some indirect effect on population growth rates' (Platt & Lamshead 1985). We would now modify this definition to include *any* process which results in a decrease in species populations, e. g. by forced emigration, or by inhibiting immigration.

NEUTRAL MODELS AND HYPOTHESIS TESTING

A 'model' as defined by Lincoln et al. (1982) is 'A mathematical formulation intended to represent a natural phenomenon or system'. The key word is 'represent' since models cannot recreate reality in all its complexity but are 'abstractions and simplifications of reality' (Green 1979). Simplification is an acceptable scientific methodology for analysing complex systems provided the simplified model mimics the complex scenario except, in the case of a neutral model, for the phenomena under investigation. In other words a neutral model must be neutral for the principle being tested and must not bias results because of unrealistic reactions to processes not under test. Thomas & Foin (1982) warned that 'Careful attention must be paid to ensure that neutrality is properly developed... and that the model itself does not exhibit behaviour pe-

cular to its own structure'. Hedgpeth (1977) described a number of pitfalls associated with modelling.

Many neutral models have been used by ecologists on a variety of organisms to test for biotic interactions. Some of those published since 1976 are listed in Table 1. All have adhered to the principle that they compare a pattern produced by a stochastic process with a pattern found in the real world. If the patterns do not differ significantly the null hypothesis cannot be falsified, so there is no evidence of a causative agent. So in its simplest form the neutral model methodology is simply a variant of the hypothetico-deductive method: it is difficult to draw a line between a 'neutral model' and a 'null hypothesis'.

Neutral models can be more complex and assume certain causative agents while testing for others. For example, the model devised by Innis & Haefner (1980) is not entirely stochastic to biotic interaction, since it includes predation, but competition is not represented so the model was used to test the hypothesis that competition is a causative agent in the organisation of communities.

THE CASWELL NEUTRAL MODEL

The principles of neutral models were discussed in some detail in Caswell's (1976) paper on community structure: the work has had a major impact on the use of models in ecology (e. g. Innis & Haefner 1980,

Matthews 1982, Thomas & Foin 1982). Using a neutral model, Caswell demonstrated the importance of biotic interactions in structuring communities and falsified the hypothesis that such interactions always cause an increase in species diversity. In fact, he found that the opposite occurred: 'communities in which biotic interactions should be able to express themselves to their maximum extent are significantly less diverse' than neutral model predictions.

Caswell (1976) discussed 3 neutral models but the one considered in this paper is a computer model originally constructed by Ewens (1972; see also Karlin & McGregor 1972) for testing a genetic theory for selectively neutral alleles. The model as used in ecology is intended to be neutral with respect to all forms of interspecific interaction (including predator-prey, herbivore-plant, host-parasite, symbiosis and competition) and interspecific differences in response to the environment. The Ewens/Caswell model gives a diversity prediction for a 'neutral' sample, allowing deviation of a real sample diversity from neutrality to be calculated by the following formula:

$$V = [H' - E(H')] / SD(H')$$

where V = the deviation statistic; H' = the Shannon diversity index; $E(H')$ = the diversity predicted by the neutral model; $SD(H')$ = the standard deviation of diversity.

Various ecologists have utilized this model. Gray (1978) used the $E(H')$ predictions given in Caswell

Table 1. Some recent publications utilizing neutral model analysis

Authors	Organism	Null hypothesis accepted (+) or rejected (-)
Caswell (1976)	Various	-
Simberloff (1976)	Arthropods	+
Caswell (1978)	Various	-
Gray (1978)	Meiofauna	-
Taylor (1979)	Bactiverous ciliates	+
Hubbel (1979)	Trees	+
Crowder (1980)	Lizards	+
Joern & Lawlor (1980)	Grasshoppers	-
Lawlor (1980)	Various	-
Innis & Haefner (1980)	Lizards and small mammals	+
Warwick (1981)	Meiofauna and macrofauna	+
Rainer (1981)	Macrofauna	-
Thomas & Foin (1982)	Various	-
Matthews (1982)	Minnows	+
Hanski (1983)	Dung beetles	+
Georgian & Wallace (1983)	Insects	-
Hansson (1984)	Perch	-
Warwick & Gee (1984)	Meiofauna	-
Schum (1984)	Bats	+
Platt & Lamshead (1985), Lamshead (1986)	Meiofauna and macrofauna	-
Castel (1985)	Meiofauna	+

(1976) to investigate the structure of meiofauna communities. Warwick (1981) compared the $E(H)$ predictions of Caswell (1976) with actual diversities for meiofauna and macrofauna but could find no evidence for deviation from neutrality. Rainer (1981) ran the computer model on data for benthic fauna from a small estuary. He was able to detect an ecotone point which had diversity values which were in agreement with neutral model predictions while areas consistent with increased biotic interaction displayed reduced diversities. Hanski (1983) repeated Caswell's (1976) comparison of tropical and temperate communities using data for dung and carrion beetles (Scarabaeidae) but was unable to confirm that tropical communities displayed a reduced diversity. Warwick & Gee (1984) contrasted meiofauna samples from 3 sites and reported that diversity was lowered in the site where competitive exclusion was more likely. Castel (1985) investigated the community structure of meiobenthic assemblages of a lagoon ecosystem. Diversity was not different from that predicted by the neutral model and he concluded that community structure was mostly controlled by physical factors. Finally, Platt & Lambshead (1985) and Lambshead (1986) applied this model to a variety of benthic meiofauna and macrofauna samples and concluded that V' appears to be a sensitive tool for the elucidation of the effects of disturbance on species abundance patterns'.

IS THE CASWELL MODEL NEUTRAL?

Ugland & Gray (1983) levelled a number of criticisms at the Caswell neutral model. They suggested that the 'model is far from neutral' and that it 'should be used as a yardstick for interspecific competition and not for neutrality'.

If true this would invalidate any use of the model as an indicator of biotic or physical disturbance. Essentially, Ugland & Gray (1983) based their case on the observation that the model has a fixed number of individuals, so a species can only become more abundant at the expense of other species. As Ugland & Gray (1983) rightly noted 'abundances therefore are negatively correlated . . . i. e., any increase of one species decreases the abundance for all other species'.

Caswell (1983) refuted this criticism, denying that the interaction noted by Ugland & Gray is competition. He replied that 'this is not competition, for the same reason that a geneticist using the same model would not consider it selection: it is not species (or genotype) dependent'. In other words Caswell was using the word 'competition' in the sense that it is normally employed in ecology as *competition between species*, where one species has some potential competitive advantage over

another due to different responses or tolerances to some factor in the environment. This meaning is implicit in such phrases as 'competitive exclusion'.

Ugland & Gray (1983) used 'competition' in a different context with an implied meaning of *competition between individuals*. This interpretation has been employed in, for example, evolutionary studies where it usually refers to competition between individuals belonging to the same rather than different species.

As we are interested in the relationship between species in this paper, rather than the relationship between individuals, the Ewens/Caswell neutral model appears to be theoretically sound for our purposes. However, as Gray (pers. comm.) has pointed out to us, semantic misunderstandings can easily occur with common English usage words such as competition and diversity. Thus it is essential to state explicitly the context in which the word is employed.

THE EWENS/CASWELL NEUTRAL MODEL AS AN INDICATOR OF PHYSICAL DISTURBANCE

In an earlier paper (Platt & Lambshead 1985) we used the neutral model as a 'relatively sample-size independent measure of diversity' specifically for the detection of physical disturbance. The neutral model was devised to be neutral to, and hence test for, biotic interactions and not physical disturbance. But subsequent work had indicated that there was a possibility of employing the model for this purpose. Caswell (1976) warned that 'a transient response following a severe perturbation or a change in external conditions might result in disagreement with the neutral model predictions' and Caswell (1978), when considering a predator-prey model, concluded that 'There is no reason why this function [effect of predation] must be performed by an actual predator. Physical disturbance would serve equally well'.

So how can physical disturbance and biological interactions such as predation give interchangeable results on a neutral model? The explanation is that disturbance is an *effect*, not a causative agent or process, or as Abele & Walters (1979) noted 'stress is defined by its effects'. And the 'effect' can be the same as that produced by biological interaction.

In other words this neutral model analyses patterns divorced from processes, which may well be advantageous. Wiens (1984) stated that 'The mission of community ecology . . . is to detect the *patterns* of natural systems, to explain them by discerning the causal *processes* that underlie them, and to generalize these explanations as far as possible'. Eldredge & Cracraft (1980) in a discussion of pattern and process in a phylogenetic context noted that 'Initially . . . the study

of pattern must be divorced as much as possible from the study of process, to provide an unbiased baseline for the evaluation of alternative hypotheses about process'. Process-oriented analysis through circular reasoning can lead to hypotheses which are tautological and hence non-falsifiable or, as Eldredge & Cracraft (1980) suggested, to a 'rabbit warren of untestable story-telling'.

For example, Abele & Walters (1979) observed that the stability-time hypothesis (Sanders 1968) was not tested against a null hypothesis nor was a test which could falsify the hypothesis suggested. These authors suggested a stochastic null hypothesis – that the patterns in species richness observed by Sanders were the product of species/area relationships – which they could not reject, thus falsifying the stability-time hypothesis.

Hypotheses which are based on biological processes as causative agents must be tested against a more parsimonious hypothesis. Where this approach has been adopted 'very few of the presumed patterns in community structure have been found sufficiently strong to justify their acceptance as true' (Sale 1984). Often it will be convenient to test observed patterns against a null hypothesis of stochastically generated patterns. It is for this reason that we consider neutral model analysis to be a powerful tool in the elucidation of biological patterns and processes.

SAMPLING AND THE EWENS/CASWELL NEUTRAL MODEL

The neutral model is highly effective as a relatively sample-size independent indicator of disturbance because 'it has a well developed sampling theory' (Caswell 1976). As Caswell noted, a sample is described by 3 pieces of information: number of species, number of individuals and the relative abundance of each species (i. e. equitability). For a given sample, the number of individuals and the number of species are known and the model calculates equitability assuming neutrality for a particular sample. This calculation can then be compared with the actual sample to give a comparison of the real sample equitability relative to the estimated neutral equitability. In other words the *V*-statistic gives a measure of whether the diversity of a sample is higher or lower than might be expected assuming neutrality. This result is assumed to reflect a similar relationship in the community from which the sample is drawn but gives no absolute measure of community diversity.

Thus *V* is 'a relatively sample-size independent measure of diversity' (Platt & Lamshead 1985) because it is a relative rather than an absolute measure. Most diversity indices give an absolute measure of the

diversity of a sample which is assumed to represent the diversity of the parent community (ecologists rarely work with a full census of a community for obvious logistical reasons). So if the diversities of communities are to be compared one is forced to contrast the diversities of samples drawn from the communities. Diversity indices are sample-size dependent so if the samples drawn from the communities differ in size then differences in community diversity may be confused by sample-size effects.

The Caswell model is only 'relatively' independent of sample size because there are some limitations. The sample must be small relative to the total size of the population because it is sampling without replacement (Ewens 1972, Caswell 1976). But the sample must be reasonably large to obtain a meaningful result. Meiofauna are perhaps more suitable than macrofauna for this type of work because it is possible to obtain a statistically large sample without destructive sampling. Because a species can never be represented by less than one individual, species drop out as a sample is decreased in size. If a sample is too small then the number of species will drop to the point where statistical significance is lost. The smallest sample we have analysed contained 50 individuals.

Sample-size independence is an important property because research into biological diversity is plagued by sample-size dependent problems at all levels. For example, Lamshead (1986) demonstrated how absolute diversity measures such as *k*-dominance curves could show a density reduction due to environmental contamination as a drop in diversity, when neutral model analysis revealed an increase in diversity. Abele & Walters' (1979) paper on species/area relationships considered a similar problem but on a larger biogeographical scale. Nevertheless, samples (as opposed to whole communities) must remain the basic ecological currency. Apart from these practical considerations Pielou (1975) concluded that even theoretically 'there is no way of estimating the evenness of a large, uncensused community that is suspected of containing an unknown number of 'odds and ends''. Unfortunately, this appears to be the situation in most benthic assemblages.

Use of the model presents a number of computational and sampling problems. Good quantitative samples are required and not all taxonomic groups provide such samples in practice. For example, many deep-sea benthic macrofauna are so dispersed that they have to be collected in sledges or trawls, which give questionable quantitative samples (Paterson et al. 1985). Some insect taxa are collected by baited traps such as light or carrion traps which give self-selected samples. For example, the Scrabaeidae data analysed by Hanski (1983) were collected in this way.

Table 2. Two artificial data sets of 5 species (A to E) with 11 and 110 individuals respectively. N : number of individuals; d : simple dominance; H' : Shannon's index; D : Simpson's index; V : neutral model V -statistic

Species	Abundance of each species	
	$N = 11$	$N = 110$
A	4	40
B	3	30
C	2	20
D	1	10
E	1	10
Index		
d	36.36	36.36
H'	1.47	1.47
D	0.18	0.25
V	+0.69	+1.84

Raw data must be used (Caswell 1976) for neutral model analysis, not data in a reworked form to fit a standardized sample size. Table 2 shows a set of artificial raw data for an assemblage of 11 individuals. Various equitability-diversity indices are calculated for this data including V , Simpson's index (D), the percentage dominance of the most abundant species (d of Shaw et al. 1983), and the Shannon index (H'). The data were then multiplied up by 10, as they might be to fit some standardized format, and the indexes recalculated. This had no effect on some diversity/dominance measures such as d or H' , or on k -dominance curves and Lorenz equitability curves (Lamshead et al. 1983). But it did have a major impact on D and V (Table 2).

However, computational problems associated with the model (Caswell 1976, Platt & Lamshead 1985) may make it impossible to run large sets of raw data. What compromises are open?

For many taxa there are accepted ways of physically splitting samples prior to analysis. But there must always be some doubt as to whether the sample-splitter has functioned adequately, i. e. it may introduce an extra source of error. And it is often by no means clear that a 25 % subsample of a homogenized sample is the same population that would be produced by a field sample 25 % of the size. This would depend on factors such as aggregation and patch size of the organisms relative to the area sampled. Nevertheless, investigations on taxa such as marine nematodes commonly employ sample splitters, including some of the nematode data used in this paper.

Subsampling the data by mathematical means also presents problems. The simplest way would be to use a random subsampler program. Table 3 shows a set of V results for some nematode samples (Lamshead 1986) and the results produced by subsamples (Lamshead 1983). The error is unacceptable and a very large

Table 3. Neutral model V -statistics for some nematode samples (Lamshead 1983, 1986) and the V s produced by 'random pick' subsamples of $N = 50$. N : number of individuals; V : V -statistics of full samples; V' : V -statistics of subsample

Sample	N	V	V'
1A	508	-1.1	-0.7
2A	549	-2.5	-1.0
3	1415	-0.5	-3.1
4A	2325	+1.3	+0.1

number of subsamples would have to be run to improve on this situation. This might solve matrix limitation problems but could require even longer processing times than running the full sample.

Caswell (1976) suggested reducing a sample by rarefaction, a method adopted by Warwick (1981). But this is also not without its problems. The original rarefaction method of Sanders (1968) was an 'ad hoc solution' with 'little probabilistic basis' (Tipper 1979). Not only is it inaccurate but the error is inconsistent, being negligible for highly dominated samples but with up to 50 % discrepancy in equitable populations (Hurlbert 1971, Fager 1972). There are accurate methods of rarefaction (Hurlbert 1971, Simberloff 1972) but these only give an estimate of species richness as the size of the sample is reduced. They do not give an estimate of the numbers of individuals in each species in the sample. $E(H')$ of the subsample can be calculated from the number of species and the size of the subsample but H' cannot. Thus the $E(H')$ of the subsample could only be compared with the H' of the full sample. As H' is sample-size dependent the error involved will vary inversely with the size of the sample and proportional to the degree of reduction.

Samples which are too small are rarely a problem: one can usually take a larger sample. But in this case there may be a temptation to add replicates together. In theory this should be sound but in practice it can be impossible to be sure that additional samples are true replicates. Adding together non-replicate samples severely biases the results by artificially increasing diversity and especially equitability. The large positive V results calculated by Gray (1978) for gastrotrich data were partially caused by aggregated samples (Rainer 1981). Hanski (1983) used pooled data of carrion and dung beetles from baited traps producing positive V -statistics for 70 % of the samples. So unlike Caswell (1976), who recorded depressed V values for tropical assemblages, Hanski found that both tropical and temperate assemblages tended towards positive values.

There is no good substitute for running the raw data from a whole individual sample when using the neutral

model. Is there then a method for analysing data which achieves the same result without the computational problems associated with the model?

ALTERNATIVES TO RUNNING THE NEUTRAL MODEL

This section considers whether there is an alternative technique which performs as well as the neutral model without incurring the computational problems associated with running the model.

Caswell (1976, his Table 2) provided a set of pre-worked neutral model results where $E(H')$ was listed for various values of sample size and number of species. Using these values it is possible to interpolate an $E(H')$ value for most samples. It is not possible to calculate V because no value is available for the standard deviation but nevertheless a comparison between H' and $E(H')$ has been found useful (Warwick 1981).

An alternative approach might be to replace the neutral model by a computationally simpler method which has been shown to correlate well with neutral model results. The model calculates a distribution (actually a log-series) for a sample (of given size and number of species) which satisfies its criterion of neutrality. As number of individuals and number of species are fixed the model actually compares equitability, a component of diversity. Can then some form of equitability measure be used as a replacement for the model?

Values of d , D and J' (an equitability index derived from H' ; Pielou 1975) were calculated for the 4 sets of benthic data used in an earlier investigation of the

Table 4. Values of V , d , D and J' calculated for the Clyde nematodes (Lamshead 1986). V : V -statistic; d : simple dominance; D : Simpson's index; J' : evenness index; N : total number of individuals

Sample	V	d	D	J'	N
1A	-1.05	17	0.0798	0.7665	515
1B	-1.28	13	0.0691	0.7705	570
1C	-0.65	20	0.0805	0.7518	971
2A	-2.45	22	0.1111	0.7204	479
2B	-1.00	28	0.1051	0.7729	455
2C	-1.42	20	0.0828	0.7642	606
3	-0.52	31	0.1373	0.7042	1476
4A	+1.30	17	0.0701	0.7839	2405
4B	+0.59	17	0.0915	0.7841	608
4C	-1.41	26	0.1243	0.7089	616
5A	-1.15	32	0.1412	0.8134	51
5B	-0.08	19	0.0766	0.8390	175
5C	-0.23	14	0.0716	0.8322	175
6A	-0.38	15	0.0675	0.8256	232
6B	-0.08	18	0.0690	0.8488	152
6C	-1.22	23	0.0871	0.7975	269

neutral model (Platt & Lamshead 1985). These were: the 'Clyde nematodes' (from the Firth of Clyde, Scotland; Lamshead 1986) (Table 4); the 'Strangford nematodes' (from Strangford Lough, N. Ireland; Platt

Table 5. Values V , d , D and J' for the Strangford nematodes (Platt 1977). Abbreviations as in Table 4

Month	V	d	D	J'	N
Jan	-4.16	58	0.3458	0.5721	398
Feb	-1.01	31	0.1313	0.7350	381
Mar	-0.64	33	0.1427	0.7338	417
Apr	-1.56	38	0.1919	0.6761	406
May	-0.70	33	0.1533	0.6942	715
Jun	-0.77	29	0.1475	0.6781	995
Jul	-4.18	50	0.2771	0.6571	158
Aug	+0.26	24	0.1294	0.7801	237
Sep	-1.54	40	0.1872	0.6762	595
Oct	-1.47	48	0.2628	0.6257	410
Nov	-2.02	36	0.1807	0.6548	683
Dec	-5.60	72	0.5261	0.4085	462

Table 6. Values V , d , D and J' for the macrofauna (Pearson 1975). Abbreviations as in Table 4

Year	V	d	D	J'	N
1963	+0.78	14	0.0414	0.8557	9 13
1964	+2.65	10	0.0376	0.8708	1 355
1965	+0.67	23	0.0812	0.7707	2 047
1966	-	16	0.0618	0.8157	1 240
1967	-0.32	22	0.1201	0.6884	1 831
1968	-1.35	25	0.1286	0.6324	2 961
1969	-2.61	64	0.4232	0.4868	1 970
1970	-	81	0.6642	0.2588	27 425
1971	-	63	0.4464	0.1227	30 874
1972	+0.40	40	0.2953	0.6180	972
1973	-	63	0.4962	0.0627	9 157

Table 7. Values of V , d , D and J' for the foraminiferans (Goody 1986). Abbreviations: \bar{x} , mean; SD: standard deviation; others as Table 4

	Depth of sample (cm)				
	0-1	1-2	2-3	3-4	4-5
V \bar{x}	-3.17	-1.99	-0.57	-0.68	-0.78
SD	0.59	0.85	0.58	1.01	0.79
d \bar{x}	14.50	20.17	18.67	25.67	25.67
SD	2.81	7.60	6.16	8.58	8.88
D \bar{x}	0.0413	0.0743	0.0554	0.1122	0.0918
SD	0.0067	0.0348	0.237	0.0396	0.0419
J' \bar{x}	0.8436	0.8510	0.8681	0.8766	0.8961
SD	0.0130	0.0390	0.0449	0.599	0.0552
N \bar{x}	349.50	104.67	67.50	40.67	29.17
SD	61.58	35.90	21.59	12.93	11.65

1977) (Table 5); the 'macrofauna' (from Loch Eil, Scotland; Pearson 1975) (Table 6); and the 'foraminiferans' (from the Porcupine seabight, NE Atlantic; Gooday 1986) (Table 7). ' d ' was selected as a simple but effective measure of equitability (May 1975; Shaw et al. 1983). ' D ' is a diversity measure which is biased towards equitability (Smith et al. 1979, Lamshead et al. 1983) and which has a simple unbiased estimator which makes it less affected by sample size problems than, for example, ' H ' (Blyth 1958). It would not be sensible to include ' H ', as ' V ' is a measure of the number of standard deviations away a theoretical ' H ' is from the actual ' H '. However, ' J ' is an equitability index derived from ' H '.

Table 8. Correlation coefficients between various indices for the 4 data sets (Tables 4 to 7)

	V	d	D
Clyde nematodes			
d	-0.34		
D	-0.40	0.92	
J'	0.45	-0.42	-0.56
Strangford nematodes			
d	-0.94		
D	-0.92	0.98	
J'	0.87	-0.94	-0.96
Macrofauna			
d	-0.78		
D	-0.72	0.98	
J'	0.87	-0.92	-0.91
Foraminiferans			
d	-0.76		
D	-0.64	0.96	
J'	0.82	-0.86	-0.69

Table 8 shows the correlation coefficients for the equitability indices and V for the 4 data sets. The degree of correlation varies quite markedly from set to set, being generally low for the Clyde nematodes but generally high for the Strangford nematodes. The greater the range for the indices the higher the degree of correlation.

D is always highly correlated with d , even for the Clyde data (0.915). This is unsurprising because Simpson's index is 'heavily dependent on the dominant species' (Smith et al. 1979) and demonstrates how effective mathematically simple indices (such as d) can be. ' J ' always correlates most closely with D or d . V correlates most closely with ' J ' on 3 of the 4 data sets (the exception being the Strangford nematodes where the highest correlation is with d and D respectively). It is noticeable that the lowest correlation between an index and its closest neighbour is always obtained

between V and another index for all 4 data sets. It can therefore be concluded that V is the most isolated of the 4 indices tested.

However, in much diversity work biologists are more interested in the ranking of stations according to their diversity rather than an absolute numerical value. Indeed, it is a matter of conjecture whether absolute diversity has any meaning – certainly it is not a property of a system in the same sense as, for example, temperature. The Clyde data are useful for testing the ranking properties of the different indices because they were collected to test the hypothesis that sub-catastrophic levels of pollution can be detected by analysis of marine nematode assemblages. To this end 9 samples (4A, 4B, 4C, 5A, 5B, 5C, 6A, 6B, 6C) were taken in areas suffering contamination, while 7 reference samples were taken in uncontaminated areas. Lamshead (1986) concluded, using a variety of techniques including non-diversity methods, that the nematode assemblages in contaminated areas had suffered a pollution effect and that equitability was increased in samples from contaminated areas compared to samples from reference areas.

If the stations are ranked, from highest to lowest equitability, in an ideal situation one would expect the first 9 samples to be the 9 contaminated samples. Therefore, a count of the number of contaminated samples in the first 9 gives a measure of the efficacy of the index. Table 9 shows the first 9 ranked samples for each index and the number of contaminated samples in the first 9.

There is little general agreement in the detailed rankings for the 4 indices. However, the number of contaminated samples included in the first 9 is enlightening. ' J ' outperformed the other indices, including V .

Table 9. The first (of 16) Clyde nematode samples ranked in order of decreasing equitability according to each diversity index. Abbreviations: * contaminated; others as Table 4. The number of contaminated samples (out of 9) is listed on the bottom row

Rank	V	d	D	J'
1	4A*	1B	6A*	6B*
2	4B*	5C*	6B*	5B*
3	5B*/6B*	6A*	1B	5C*
4	–	–	4A*	6A*
5	5C*	1A/4A*/4B*	5C*	5A*
6	6A*	–	5B*	6C*
7	3	6B	1A	4B*
8	1C	5B	1C	4A*
9	2B	1C*/2C*	2C	2B
No. of contaminated samples	6	6	5	8

One cannot read too much into one small set of data but it can be safely concluded that, if ranking is important, the V -statistic did not outperform the simpler equitability indices although it gave a similar result despite its isolation from the other indices (Table 8).

Lamshead (1986) concluded that equitability was higher in the contaminated samples by demonstrating that the V -statistics for the 9 contaminated samples were significantly different from the 7 reference samples at the 5% level (Student's t -test). If this test is repeated using the simpler equitability indices, d and D show no significant differences between the samples but J' shows a significant difference at the 1% level.

The Strangford nematodes test a more complicated situation (Fig. 1). These data are a monthly time series from a station at the high water mark on a sandflat. The

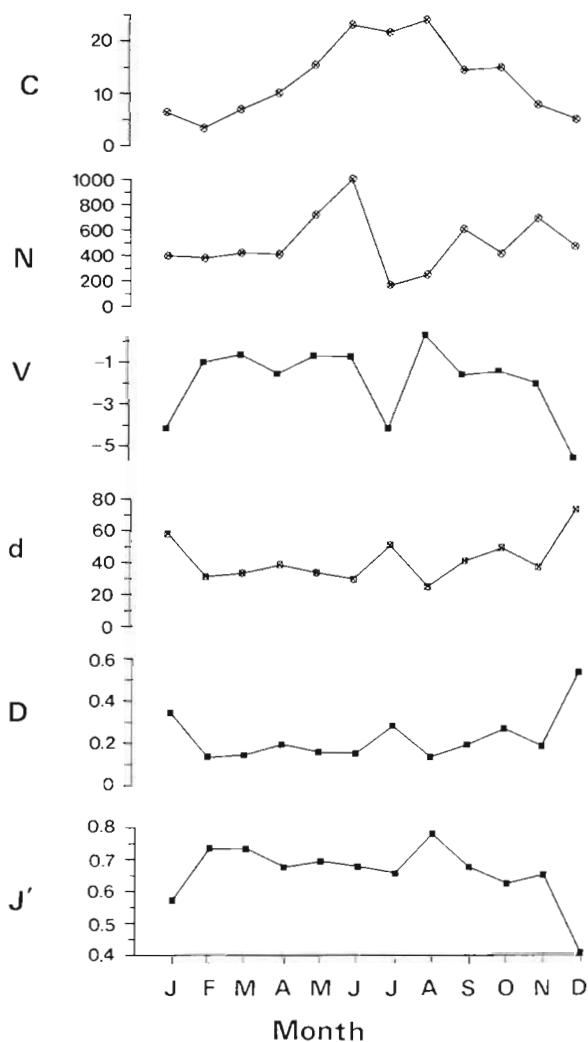


Fig. 1. Equitability indices for the Strangford nematodes (Platt 1977). Y-axis: C, temperature in °C; N, number of individuals in sample; V, neutral model V -statistic; d , % dominance of commonest species in sample; D , Simpson's index; J' , evenness index

marine nematode assemblage here is subject to natural stress. The number of individuals per sample (N) suggested that there was an overwintering population which started to increase in numbers in summer, possibly due to greater resource availability. Density peaked in June, suffered a catastrophic collapse in July, and returned to the overwintering population density in the autumn.

The V -statistics appear to reflect this story. In January, this was a heavily stressed assemblage with an extremely low V -statistic of -4.16 . As the year continued V increased to a level of about -1 which continued through the population increase in May and June. Because the population was increasing it seems likely that this negative V was due to competitive exclusion rather than disturbance. When the population crashed (possibly due to temperature-related disturbance) the V -statistic was again extremely low, at -4.18 . After the crash, the V -statistic was positive, indicating that the surviving population had an abundance of resources and hence competitive exclusion was not operating. Once the population increased competitive exclusion reasserted itself and V dropped back to around -1.5 . When winter arrived, V fell to -5.60 .

Our confidence in this interpretation is increased by the fact that the shape of the curves for the other indices tends to support the hypothesis, and certainly does not contradict it by providing a more parsimonious explanation. But if the other indices tell the same story, was it worth the tedious calculations required to obtain V ? In this case the answer must be yes. The other indices merely show trends, rising and falling figures. Because the V -statistic is calibrated against neutrality it can give a much greater insight into the processes behind the observed patterns. For example, V -statistics of -4 and -5 are extremely low indicating considerable disturbance while positive V s are indicative of over-equitability apparently indicating an undisturbed assemblage with an abundance of resources. These conclusions could not have been arrived at merely by recording one of the simpler equitability indices.

The macrofauna data resemble the Strangford nematodes in that they are a time series from a single station, in Loch Eil (Fig. 2). But in this case the disturbance effect was caused by pulp mill effluent. The V -statistics in Platt & Lamshead (1985) appeared to tell a similar story to the Strangford nematode data. The benthos started at a positive resting level, declined as the disturbance increased, and swung back to positive again as soon as the disturbance declined. However, some V -statistics are not available due to computational problems with large data sets, reflecting the major drawback of this technique. The pre-contamination resting levels are positive. The explanation for this is not clear but it possibly lies in the fact that the Loch is

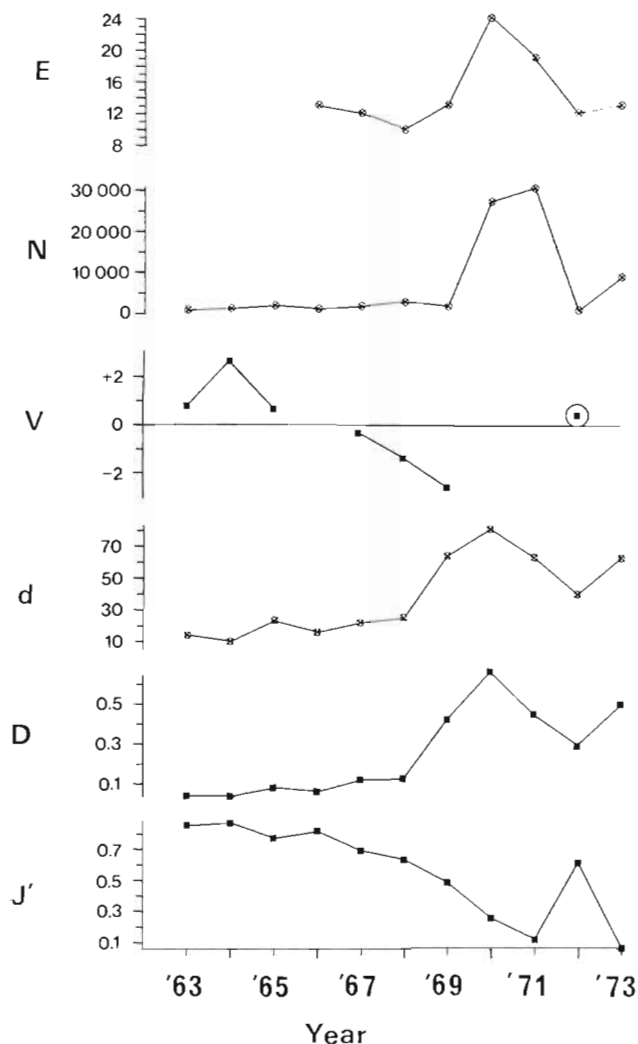


Fig. 2. Equitability indices for the macrofauna (Pearson 1975). Y-axis: as Fig. 1, but *E*: effluent discharge in tonnes per day

an enclosed area which is relatively small in comparison to the populations of organisms under investigation. There might therefore be a dearth of rare species (because 'intruders' from outside the area might be excluded) causing the species abundance patterns to more closely resemble a log-normal than a log-series. This would tend to increase equitability leading to positive *V*-statistics (Lamshead & Platt 1985, Platt & Lamshead 1985). This neat explanation is rather confounded by the fact that many of the species in question have a planktonic larval phase and the enclosed nature of the Loch may not present a barrier to planktonic larvae.

The other indices fundamentally show the same story as the *V*-statistics, which is encouraging. But as in the Strangford nematodes it would be difficult to interpret these other indices without the *V*-statistic because they are not calibrated against a neutral point. For example,

the positive *V* obtained for the 1972 data is an indication of a post-disturbance assemblage with an abundance of resources precluding competitive exclusion. It is doubtful if such a conclusion could so easily be drawn by, for example, noting that the *d* index dropped from 1970 to 1972 from 81 to 40%. Nevertheless, it is essential to calculate another index for this data to 'fill in the gaps'. The *d* index of 81% for 1970 supplies vital information.

The foraminiferan data (Fig. 3) perhaps resembles the Clyde nematode data in that it is a simpler situation covering a spatial rather than a time series. The results here are rather unusual in that the different indices tell different stories. The *V*-statistic shows a low equitability at the surface layer, which Platt & Lamshead (1985) ascribe either to disturbance or high density and growth rates (and hence competitive exclusion), rising to the level of a slightly negative *V* at depth 2 cm in the sediment. The other indices merely show random variation. This interpretation is confirmed by using Student's *t*-test. The *V*-statistics for the 0 to 1 cm, 1 to 2 cm and 2 to 3 cm layers are significantly different from each other at the 5% level. There is no significant difference (at the 5% level) between these layers for the other indices. In other words, neutral model analy-

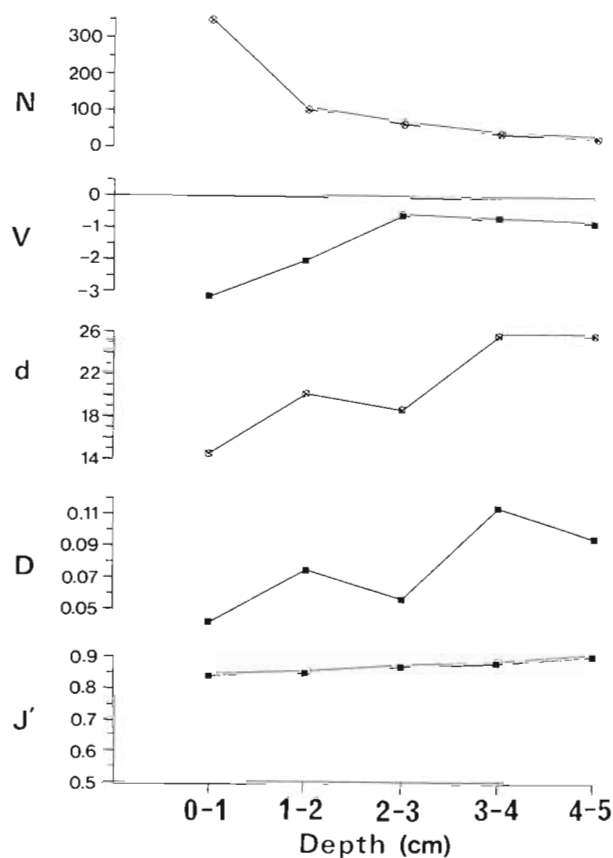


Fig. 3. Equitability indices for the foraminiferans (Gooday 1986). Y-axis: as Fig. 1

sis has a greater resolving power in interpreting these data. The explanation for this may lie with the small sample sizes in the lower sediments, as V is less affected by sample size than the other indices.

So no simpler equitability index performed overall as well as V because (a) the other indices correlate better with each other than with V , (b) the calibration of V against neutrality is highly informative and (c) V is less sample-size dependent than the other indices. Of the other indices tested J' would seem to be the best alternative to V because V is more closely correlated with it.

SUMMARY AND CONCLUSIONS

Neutral models have been reviewed and found to be a useful tool in the elucidation of biological processes and the effects of physical disturbances on ecosystems. The Ewens/Caswell neutral model in particular has had a significant influence on community structure ecology.

The Ewens/Caswell model is neutral with respect to competition between species and it can be used to test for physical as well as biotic interactions. Indeed, the model measures the effect of these processes, which are identical, and not the processes themselves. In theory, the model is superior to other simpler equitability indices because it is relatively sample-size independent. However, there are computational problems in running the computer program on some data sets. It is concluded that there is no satisfactory way of artificially reducing data sets, with the possible exception of sample splitters. Similarly, data sets should not be added together to increase sample size as equitability is also artificially increased in this way. There is no alternative to running raw data on the model even if this means being unable to run certain data.

The model outperformed simpler indices on 3 of the 4 data sets tested here and interpretation of the results of the fourth depended on exactly what question was asked of which index. V -statistics were essential to obtain the best interpretation of time series data, although simpler indices were useful in filling in the odd gap in the results produced by an inability to run large data sets. Only the neutral model was capable of detecting a trend in the foraminiferan data, probably because in the other indices the trend was masked by sample size effects. Where contaminated samples were ranked against uncontaminated samples, V performed no better than computationally simpler indices, although only V and J' were capable of showing the contaminated samples to have significantly different indices from uncontaminated samples.

It is therefore concluded that the Ewens/Caswell

neutral model is an important analytical technique for community ecology despite the computational difficulties associated with it. Nevertheless, simpler equitability indices are also worth retaining because they can be used to infer the effects of disturbance in samples too large to be run using the model. Computationally simpler equitability indices would seem perfectly adequate for routine monitoring where an uncomplicated comparison is required between test samples and reference samples.

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