

Analogue Particle and Random Packing Models of Ecological Community Formation

David Scott¹

¹ Lake Tekapo, New Zealand

Correspondence: David Scott, Lake Tekapo, New Zealand. E-mail: scott_d_hc@xtra.co.nz

Received: March 16, 2014 Accepted: June 16, 2014 Online Published: June 23, 2014

doi:10.5539/jps.v3n2p58

URL: <http://dx.doi.org/10.5539/jps.v3n2p58>

Abstract

The apparent constancy of the near linear relationship between logarithm of a species' abundance in a community and their rank order led to a brief review of existing species abundance distribution (SAD) models; a proposal of three further classes of analogue models; and an evaluation of a meta data set of empirical vegetation composition data.

A new class of models is proposed considered particle packing of circles (2D) or spheres (3D) as representing individuals of species which under different scenarios of arrival, growth, displacement and mortality determine community maximum packing and SAD.

Besides the existing random models treating each species as an entity, two further classes are added which considered dismantling rather than assembly models, or retaining identity of taxa species through successive stages of assembly or dismantling models.

In each of the models, the resulting form of the SAD was dependent on which metric of an individual (density, area, volume etc) was used as a measure of abundance.

A comparison was made between the resulting 576 different models and 432 sets of 10 species and 110 sets of 5 species empirical observations. There was a wide variation in species proportions and a lack of clustering around a particular model.

In those comparisons, the particle packing models of individuals were as good as the random models treating species as an entity and did offer a functional explanation of the formation of the SAD.

In most models and empirical data the species ranking is done retrospectively so there will always be a high negative correlation between abundance and rank implying a need for a reevaluation of the ecological significance of the relationship.

Keywords: Species abundance distributions (SAD), models, particle packing models, 2D, 3D, Soddy, geometric series

1. Introduction

One of the interesting aspects of ecology is the relative constancy in the proportional abundance of different species in a community, with the generality that they are often well described by a log/linear relationship irrespective of the species involved. When the relative total abundance of species in a community are expressed on a logarithmic scale and species are ranked from the most to the least abundant on a linear scale, there is generally a strong near-linear relationship between the two, irrespective of the environment, communities or species being considered.

This is an active continuing world-wide topic and research has gone through a number of stages starting with the accumulation of empirical data showing an apparent consistency in these log /linear species abundance distributions (SADs). The initial stages were finding mathematical functions which mimicked those relationships e.g. geometric series or log series.

Some of these were statistical (e.g. normal, truncated log normal) leading to consideration of statistical based simulation models. Several use the ecological assembly analogue of successive species colonizing a domain or new environment, with the proportion they take-up related to some probability. Also implicit in several of those models is that a species, as an entity, arrive in order of their size or suitability as indicated by their final

abundance. Also, in several of those, it was necessary to define some of the characteristics of the species. As the characteristics considered tended to proliferate there were a counter studies in neutral theory models to question whether they were all needed.

While many of those probabilistic models give a good description in a retrospective analysis of particular species abundance data, they generally lacked an adequate functional explanation at the level of species, or individuals, of how or why those SAD's might develop.

The current research trend is towards trying to understand the SAD's in terms of the characteristics of the species involved. These may be complex microclimate / physiologic models for some species systems where there is adequate known detail. More generally there is the attempt to determine a common series of morphological and/or physiological characteristics (functional traits) which can be simply measured on a large range of species and which are believed to be relevant in determining their proportions in a community (e.g. Diaz et al., 2004).

Associated with that has been the inclusion of the mathematics of entropy information considerations of the second law of thermodynamics, and the Boltzmann distribution law (e.g. He, 2010). Application of those concepts give the most probable proportions of 'species' in a community, subject to the twin trend of all systems trending to random disorder, versus functional constraints on that process (in the present context, the different specified functional traits of the species involved and the species proportions needing to sum to some constant value). This is the MaxEnt models being developed by a number of investigators (e.g. McGill et al., 2006; Shipley, 2009; He, 2010; He & Zillio, 2010; Roxburgh & Mokany, 2010).

The mathematics of the entropy method are neutral. What are the relevant functional traits giving constraints in a particular situation and what are the interpretation of the results depend on biological variables included and ecological considerations. They also depend on knowing the values of the functional traits for the species considered and the model also consider species as a collective entity of individuals.

In the context of such models, this paper offers a different perspective - that the relevant functional trait may be the occupation of space. The suggestion made here is that community formation may related to the actual (or conceptual) relative size of individuals of different species and the manner in which they can be collectively packed into a given domain space and that the frequencies of different sizes relate to their interaction, as in competition, to achieve maximum overall packing. The hope was that this approach may suggest an alternative functional reason for species proportions in a community.

The analogue to be used is of the packing of individuals of different sized species as circles in 2D to represent area (e.g. ground cover of species in a vegetation), or the packing of different sized species as spheres in 3D to represent volume or mass of individuals of species and their cumulative total contribution. Enquist and Niklas (2001) have simulated light interception of vegetation using a combination of 2D and 3D considerations.

Similar consideration of what determines the density and maximum packing possible of different sized objects occur in mathematics (e.g. Dodds & Weitz, 2002); molecular chemistry, crystallography, in geology in sediments (e.g. Petijohn, 1975), in engineering in aggregate packing, concrete and ceramics (e.g. Sohn & Moreland, 1968; Stroeven & Stroeven, 1999), in commercial packing and in marketing resource space (e.g. Peli & Nooteboom, 1999). The first class of models described here explores some of the concepts and results from those fields to the relative species abundances and community formation in ecology. Also, as in ecology, investigations in those other fields have found that log-normal size distributions are common and its possible applicability to ecology came from a ceramics background (Preston, 1948).

The analogue simulation models were developed from several different perspectives of: whether the packing occurred with individuals at their final size if there was space available; or whether allowing initial insertion at a small size (e.g. seed) and allowed to grow; whether mortality occurred if they could not grow; or different displacement rules if they were potentially larger than surrounding individuals; or whether the placement was random or in some more regular pattern. They also considered how packing and rank relationship might differ between considering size alone (as a neutral approach) or prior designation into different species of different potential sizes.

While the simulation models used the packing scenario, the focus was on the changing species abundance distributions (SAD's). If they simulated the log/linear or geometric trends observed in ecological data then they offered a functional explanation.

The next class of models considered was to run similar simulations of some of the various present probabilistic assembly models which consider the probability for the arrival of a species as entities. This is followed by a suggested further class where there may be an equivalent range of dismantling models corresponding to the

ecological analogy of species thinning or being lost or replaced in a community through changed environment or species suitability.

In most of the models and empirical data the rank ordering of species is retrospective. Another class of models considered retained the identity of taxa species through successive stages of assembly or dismantling models.

The paper describes and evaluates these suggested particle packing, assembly and dismantling models, outlines their resultant density/packing and SAD's. The simulations also prompted discussion on issues of: species or size?; individuals or collective for a species?; retrospective or a priori definition of rank?; and what is the most appropriate measure of species 'abundance' metric in such different relationships within a community?; - density of individuals?; their cumulative area; volume or mass?; or some other metric.

2. 2D Random Loose Packing With Uniform Size Decreases

2.1 Simulation Models – General Parameters

The initial set of models used a random placement of individuals and 'loose' packing, in the sense that the initial placement of an individual remained fixed with no allowable reshuffling of position as other individuals arrived or grew. The scenario was plant oriented, of random arrival of species at a point as a small propagule (e.g. seed), becoming rooted, with their subsequent growth in increments up to a maximum size for an individual, subsequent mortality and release of space if individuals had reached their maximum size or prevented from expansion because of conflict with adjacent individuals for a set number of occasions.

The models considered a set of ten species of different potential maximum sizes. These were arbitrarily chosen as radii in decreasing integer steps of units from ten to one.

The models considered an arrival stage and followed by a possible growth stage if space was available relative to previous arrived individuals. The arrival stage was a random uniform selection from a list of available species and by implication their possible maximum size (radii). In the models described, species had equal probability of selection for consideration, but easily alterable to allow for different probabilities for selection. In static models the individuals were inserted at their maximum allowable size, whereas in dynamic growth models an individual could occupy a site at initially zero dimensions (radii=0) and subsequently grow. For the growth stage there was random uniform selection of an individual for consideration from among already present individuals of all species. The selected individual was allowed to increase its radii by one unit if there was space available. If not its radii remained the same but a record was kept of the number of times it had been selected and denied growth at that radii size.

In the 2D models the coordinates of the centres remained fixed as an analogue of a fixed establishment point for a plant seed or propagule. The 3D models simulated vegetation in that the individual sphere similarly remained in contact with one point on one of the 2D planes (e.g. ground surface) but that the centre could rise as the individual grew. The analogy was extended to include a 'stem' from the centre to the ground centre point and at some multiple of the radii external of the sphere but having the same overlap restrictions as the sphere (i.e. the 'stem' of one individual could not be overlapped by the canopy sphere of another)

The concept of life-span or mortality was introduced by placing a restriction on the number of times an individual was selected but failed to find room to grow. Three alternatives were modelled: that the maximum duration was the same for all individuals (arbitrarily used the value of 5), or that it was the maximum allowable size for the species (i.e. that smaller species have shorter life-spans), or that life-span was proportional to current size irrespective of species (smaller individual generally more prone to mortality – using the limitation of the current radii of the individual).

The general criterion used was that an individual could touch but not overlap the space occupied by any other individual. In the arrival stage an individual was not accepted if it over-lapped the domain of any other individual already present. However, alternatives were modelled in the growth stage. The first was where any other individual could block the potential growth of the selected individual – irrespective of their relative sizes. The other two alternatives were where there was possibility of replacement (competition) if all potentially overlapped individual were smaller than the proposed increase in size of the selected individual. The two alternatives were whether the potentially overlapped individuals were equal or smaller than the proposed growth, or just smaller. As an analogue of ecological processes the restriction that individual could not overlap was appropriate for individuals such as animals, but somewhat ambiguous for plants in vegetation where there may be mixed canopies.

In most models there was alternating selection of new individuals for potential inclusion and selection of an existing individual for growth. The exception(s) were the self-thinning models where the initial phase was the random placement of a high number of individual of zero size (radii = 0), followed by repeated selection among those for the growth phase.

The radii of individuals and their growth were programmed in integer increments.

The models were simulated on a base 100 x100 grid size (= ground area) of radii units. As this was still a 'small' sample relative to some infinite domain, a further 'buffer' zone of five units was included on each side. The random coordinates for centres were selected within this extended grid at discrimination of at least less than 0.001 of radii units (selection near radii unit size would have had an indirect effect of implying a square packing).

A running record was kept of each individual's species identification, its centre position, current radii and duration at that size. As the models are stochastic in nature, each of the models was simulated at least five times. At a summary stage the data was confined to individuals that had centres within the base 100x100 grid and along two adjacent boundaries.

Most of the results presented are after between fifty and a hundred and fifty thousand iterations. The computing time to achieve a similar number of iterations could also be viewed as an analogue of community development time. The results are given for the packing/density and the SAD for both species and size of individuals independent of their species designation.

The abundance of species can be presented either as proportions of the total domain or space occupied, or as proportions of the collective total for the number of species considered, or as proportions relative to the most abundant. The relative relationship between the species will remain the same for all three configurations. Throughout, this paper has principally use the third configuration of expressing the abundance of lesser ranked species relative to the first ranked species (=100) for ease in comparing alternatives models in graphical presentation (Whittaker plots –Ulrich et al., 2010).

Proportions are relative not absolute e.g. the gain of one species in a model would automatically decrease the proportions of the remaining species even if there may be no implied change in their absolute abundance. Consideration will be given in some models of the use of proportions as surrogates for abundance.

The various models to be described have been given a common compound four-level coding as appropriate to reference in text, tables and figures. The first is a leading 25-class, lower-case letter code based on their similarity in the resulting SAD and interest in subsequent comparison with empirical observations in the meta-data comparison. The second is an upper-case letter code for model type and is approximately comparable for the 2D and 3D models. The third is a lower case letter code for the random packing particle models indicating whether the relationship is with individuals' radii (*r*) or species designation (*s*). The fourth is a lower case letter for which is the relevant abundance metric – density (*d*), linear (*l*), area (*a*) or volume (*v*). The coding in figures uses dashed line for density and solid line for area (2D) or volume (3D). Models that had only small differences in their SAD were combined for presentation.

2.2 Packing (15×3 Models)

A comparison between fifteen 2D models differed in their parameters and consequential packing and SAD (Table 1, Figures 1 and 2). These were in three groups: comparatively static models where individuals of ten species were inserted directly at their final size, but differing in the options of later arrivals displacing earlier arrivals (models B, C, D); dynamic models where there was alternating selection between arrival of ten species at zero size, potential growth to their maximum size for each species, differing displacement options, and differing duration before mortality (E, F, I, J, O); and dynamic self-thinning models where there was a high number of initial arrivals of zero size and subsequent potential growth, displacement and mortality (models R-T, L for a single species and models Y, W for ten species).

There was a wide difference between the mean size of individuals, density and total packing achieved after a similar high number of iterations of each model (Table 1, Figure 1). There was the expected general inverse relationship between mean size (radii) of individuals and cumulative density.

The minor scale fluctuations in the presented results are random stochastic fluctuations in the combined results from the five simulations averaged for each model. The coefficient of variation of the tenth ranked species from the different simulations is given in the tables.

The total packing was low at between 40-60% for most of the models after the fifty to a hundred and fifty thousand iterations used. This random packing compares to the theoretical 78.5% for regular square packing, or 90.7% for regular triangular packing of uni-sized circles. The trend differed between the models (Table 1). Three of the relatively static models with insertion of individuals at final size (A, B, D) were still increasing in total packing when iterations stopped – with some iterations reaching 85% packing.

An exception was model F for insertion at zero size, growth, but where potential growth was stopped by any overlap

with any earlier individual, including any occupancy of zero size. The model indicated a rise to an initial maximum density and packing but with both subsequently decreasing when iterations were stopped (Figure 1 F1, F2).

The general trend in most models was for abundance of the largest potential species or size to be first ranked when the metric was area, and successive ranks for successively smaller potential species or sizes (and later similarly for 3D volume abundances). The exceptions will be noted in relation to particular models. The converse occurred when density was the metric, that the smallest species or sizes were first ranked with successive ranks for successive larger species or sizes. The implication is that as the abundance metric used changes from density through to density by linear, to area (to volume for 3D) that there were intermediate stages where a metric could indicate similar contribution from different species or sizes, as indicated by a low gradient of the SAD. The metric which gave the minimum gradient for each of the models is presented in the tables.

Table 1. Coding, parameters and output characteristics for different random 2D loose particle packing models of circles with uniform decreases in potential radii sizes*

Code	Nsp	Dis	M	T	Size	Gradient		CV10		Size/abundance					
						Sp	R	Sp	R	Species			Radii		
										d	l	a	d	l	a
Insertion at final size and no mortality															
A	1	n	.	i	5.0	
B	10	n	.	i	1.5	a	.	120	.	++	+	?	++	+	?
C	10	le	.	f	5.2	d	.	90	.	?	+	++	?	+	++
D	10	lt	.	i	2.6	a	.	89	.	-	?	?	-	?	?
Alternate random arrival and growth															
F	10	n	5	d	1.2	a	a	8	.	u-	u-	?	u-	?	?
E	10	le	5	d	3.9	l	l	28	.	--	u-	+	u-	u+	+
O	10	lt	5	d	3.1	a	l	.	.	--	u-	u+	u-	u	+
I	10	le	sp	d	4.0	l	l	27	49	-	?	+	u-	u+	+
J	16	lt	sp	d	3.8	d	l	47	35	.	?	?	++	u-	u+
Self thinning – 1 species															
R	1	le	5	d	6.8	.	l	.	83	.	.	.	^	u+	?
S	1	lt	5	d	6.2	.	l	?	?	?
	1	le	hi	d	6.8	.	a	.	50	.	.	.	?	/	?
T	1	lt	hi	d	7.2	.	l	.	38	.	.	.	u-	?	u+
Self thinning – 10 species															
Y	10	n	5	d	6.0	d	d	.	.	.	?	++	?	+	++
W	10	le	5	d	5.9	d	d	104	112	?	+	++	+	++	++

*Nsp. = Number of species considered; Dis = Displacement criteria (n = any potential overlap stops growth, le = can displace if all potential overlapped individuals are equal or smaller, lt = only if all smaller); M = Mortality - allowable duration at one size before deletion (5, sp = maximum species size, hi = 1000). T = Trend in packing/density relationship at presentation stage (i = packing continuing to increase, f = fluctuating around some mean value, d = packing decreasing); Size = Mean radius size of individuals as percent of largest. Grad = Abundance metric giving minimum gradient of SAD (Sp = for species, R = for radius, d = density of individuals, l = linear (density x radius), a = area, v = volume). CV10 = Coefficient of variation of 10th ranked species between different runs. Relationship between individuals and overall abundance for different metrics (++ = largest species or size strongly dominant; + = moderately dominant; u+ = U distribution tending to largest size; u- = U distribution tending to smallest size; ? = no clear pattern; ^ = inverted U with intermediate size dominant; - = smallest species or size moderately dominant; -- = strongly dominant).

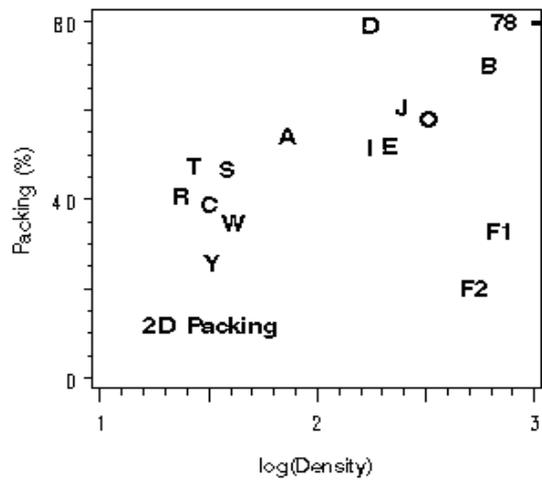


Figure 1. 2D random loose packing models comparison of packing/ density relationship of after a similar number of iterations. Model coding as in Table 1

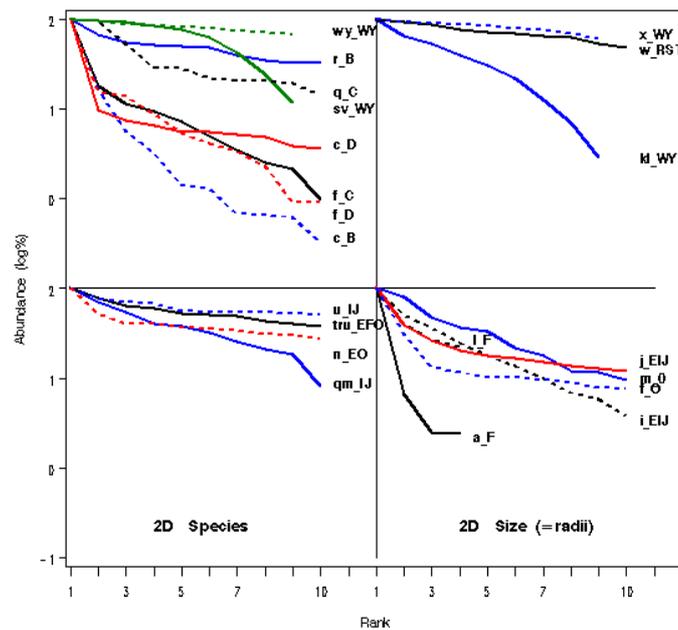


Figure 2. 2D random loose packing model species abundance distributions (SAD's) either as species (left side) or radius sizes (right) and abundance as either density of individuals (--) or as cumulative circle area (___).

For the relatively static models (B-D) where individuals were inserted at their final size the SAD were the same whether species or size distributions are considered.

The more dynamic models (E, F, I, J, O) for ten species alternated random insertion at zero size, random selection for growth to a maximum size, and deletion/mortality based on duration at one size.

Models E & I were taken as the reference as possibly the most realistic analogue of a developing vegetation cover, with other models being a sensitivity analysis of effect of parameters around that reference. That reference model had mortality of an individual if duration at one size exceeded five occasions, and allowable displacement if a potential individual's size was larger or equal to all surrounding individuals.

In model B individuals were randomly inserted at their final size and their insertion stopped if they potentially over-lapped any previous individual. In the early iteration stages species and sizes had similar probabilities of finding

space (and this was common to most models). But as iterations proceeded there was increasingly less probability of large individuals finding space and an increasing probability of only small individual finding space leading to a high density and also high packing (Figure 1-B).

The self-thinning dynamic models considered only a single species (R, S, T) or ten species (W, Y) initially of high density ($\log(\text{density}) = 4$) of random insertions at zero size followed by random selection for growth to any size subject to availability of space, different displacement options, and different deletion/mortality options depending on duration at a particular size. The reported results refer to data when iterations had reached $\log(\text{density})$ of c 1.5. After a similar number of iterations the packing/density relationships were similar for models investigated (Figure 1). There was a small trend for the packing to be greater when displacement was for 'less than' rather than 'equal or less than'.

2.3 Abundance /Rank Relationships

The changes in sizes and density are reflecting in the resulting abundance/rank relationship. For model B the resulting SAD was relatively flat when the abundance metric was cumulative area, but the steepest for the 2D models when the metric was the cumulative density (Figure 2 - r_Ba cp. e_Bd).

The relationships changed if later arrivals could potentially overlap and displace earlier arrivals. The two scenarios used were where displacement was possible if none of the potentially over-lapped individuals were larger, or whether the overlapped was equal or smaller (model C) or just smaller (model D). This results in a change in the perspective of species or size ordering versus rank. In both models there was the increasing importance of the larger species or sizes, particularly the largest.

For abundance as area the largest species or size had the greatest total area and also first ranked species. There was a change of slope at the second ranked species (f_Ca, e_Da). However, with abundance expressed as density of individuals, the distributions were U-shaped with high contribution by both the smallest and largest species or sizes and intermediate for others. Thus in the re-ordering to ranks there was no clear relationship between the decreasing abundance with rank and species order (m_Cd, f_Dd). There was a large effect on density, packing, species and rank relationships between the rather subtle difference in displacement criteria between 'less than or equal' and only 'less than'.

The more dynamic models (E, F, I, J, O) for ten species had alternating random insertion at zero size, random selection for growth to a maximum size, differing displacement options, and differing deletion/mortality based on duration at one size.

Results are given for relationships after a high number of iterations. The relationships developed as the iterations increased. For example for the reference model E with initial insertion as presence, the early iterations gave a limited range of possible sizes (radii) with no pattern for difference between species or sizes as most species and sizes could find space. With further iteration, growth and displacement, the larger sizes increased and by 1K iterations the species of larger potential size were becoming dominant and that increased with further iterations. As area contribution, the trend in the SAD was for an initial slight convexity in the relationship becoming more linear as iterations increased, indicating that at an intermediate stage the larger sized individuals were making a relatively greater contribution because of displacement considerations, but that as iterations continued further smaller sized individuals had a better chance of occupying sites becoming available from mortality considerations. The reverse trend were present considering density with initial limited range in possible sizes of near similar frequencies, but changing to a trend of frequencies decreasing with increasing actual or potential (= species) sizes. This trend in the SAD for density was generally of increasing concavity as iterations continued, with a break of slope at about the third ranked size indicating the greater predominance of the first few size classes relative to intermediate and larger possible sizes (Figure 2).

The four models (E, I, J, O) with displacement options had reached a similar values of fluctuating around some mean value in packing relationship and SAD with some of the models for 'less than' rather than 'less than or equal' combined for presentation.

The density of individual was relatively uniform across all species when the allowable duration of individuals was proportional to maximum species size, with a greater density of small species if the allowable duration was similar for all species (u_IJd, n_EOd). With abundance as cumulative area, the larger species dominated, with the contrast between species being greater where the allowable duration of individuals was proportional to maximum species size (qm_IJa). The larger sizes dominated the classes considering cumulative area with relatively little difference in distribution with other size classes between the models and in their translation to SAD's (f_Ord, i_EIJra). The density of individuals in the different size classes showed a shallow U shaped distribution with a preponderance of smaller

sizes. The effect of mortality considerations, by altering the allowable duration at one size, was not large. The model F of growth and mortality but with no allowance for potential displacement of smaller by larger individuals, gave results different from other models.

Table 2. Coding, parameters and output characteristics for different random 3D ground touching loose particle packing models of spheres with uniform decreases in potential radii sizes. Output variables as for 2D (Table 1) with addition of S = parameter for an external stem as multiples of sphere radii

Code	Nsp	S	Dis	M	T	Size	Grad		CV10		Size/abundance								
							Sp	R	Sp	R	Species				Radii				
											d	l	a	v	d	l	a	v	
Insertion at final size and no mortality																			
A	1	0	n	.	i	5.0													
B	10	0	n	.	i	1.4	v	.	85	--	--	u-	+
C	10	2	n	.	i	1.4	v	.	94	--	--	-	?
Alternate random arrival and growth																			
- species maximum radius in unit decreases and equal probability of arrival																			
F	10	0	n	5	d	1.4	v	d	25	.	?	?	?	?	--	?	?	++	
G	10	2	n	5	d	1.2	v	d	6	.	u-	u-	?	?	--	-	?	?	
E	10	0	le	5	f	2.6	a	l	4	34	-	u-	u+	++	u-	u+	+	++	
H	10	2	le	5	f	2.6	a	l	15	25	--	-	+	++	-	u-	+	++	
I	10	0	n	sp	d	1.3	d	v	14	.	^	+	++	++	--	-	u-	+	
J	10	2	n	sp	d	1.4	d	a	49	.	^	+	+	++	-	?	?	?	
K	10	0	le	sp	f	2.6	l	l	13	19	-	?	+	++	u-	u+	u+	+	
L	10	2	le	sp	f	2.7	l	l	13	22	-	-	+	++	u-	u	+	++	
M	10	0	le	c	f	3.4	l	l	18	30	-	u-	+	++	u	u+	+	++	
N	10	2	le	c	f	3.1	l	l	15	30	-	u-	+	++	u-	u	++	++	
O	10	0	lt	5	i	2.2	a	a	19	106	--	-	?	+	-	?	?	+	
- higher probability of small species arrival																			
P	10	0	le	5	i	2.4	a	l	22	84	--	--	-	?	-	?	?	+	
- higher probability of large species arrival																			
Q	10	0	le	5	f	2.7	a	l	14	23	++	++	++	++	u-	?	u+	+	
Self thinning – 1 species																			
R	1	0	le	5	.	7.8	.	l	.	54					--	?	+	++	
U	1	0	n	5	.	6.5	.	a	.	154					-	u-	?	u+	
S	1	0	lt	5	.	7.6	.	l	.	22					u-	?	+	++	
	1	2	le	5	.	9.2	.	l	.	22					u-	?	u+	++	
T	1	0	le	hi	.	8.1	.	l	.	39									
Self thinning – 10 species																			
V	10	0	le	5	.	6.1	d	d	69	41	?	+	++	++	+	++	++	++	
Z	10	0	n	5	.	5.5	d	d	.	.	?	^	++	++	?	?	u+	+	
W	10	0	lt	5	.	5.9	d	d	.	29	?	u+	++	++	+	++	++	++	
X	10	2	le	5	.	6.0	d	d	.	142					?	+	++	++	
Y	10	0	le	hi	.	6.0	d	d	34	20	?	u+	+	++	u+	++	++	++	

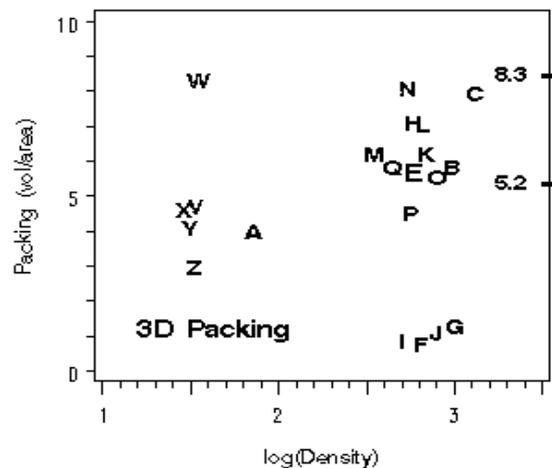


Figure 3. 3D loose packing. Packing/density relationship

The different packing/density relationship has already been referred too. In other models all species and sizes were present at the iteration stage presented, whereas in model F only four smaller sizes were present (d_{Fra}) though represented approximately equally in area contribution (a_{Fra}).

For the ten-species self-thinning models the relative density as individuals was very similar for the different species, but cumulative area was dominated by the larger species and rapidly decreasing contribution by smaller species ($wy_{\text{WY}} \text{ sd}$, sv_{WYsa}). The same trends were slightly greater considering sizes ($x_{\text{WY}} \text{ rd}$, kf_{WYra}). The single species also had a flat gradient for area (w_{RSTra}).

3. 3D Random Loose Packing With Uniform Size Decrease

3.1 Packing (27×4 Models)

Packing can have different meanings for ground-touching 3D sphere packing models. For infinite space models it would be the proportional occupation of unit space. For ground touching spheres, as in the present models, it could have been some arbitrary chosen upper limit of the height dimension, or as defined by the largest individual, either actually achieved or the maximum possible. In the present models it was defined as the ratio of the volumes occupied per unit ground area.

For theoretical regular square- or triangular touching packing of uni-sized ground-touching spheres the value are 5.23 or 8.27 respectively and the same density as for 2D packing of circles. The general packing ratio for the present random placement of spheres were mostly within those bounds even for multiple species of different sizes and or where they had ‘stems’ and could use different vertical niches (Figure 3).

For models of insertion at final size (A-C) the relative density and packing, after a similar number of iterations, was increasing from single sized species (= spheres) (A) through ground-touching multiple sized species (B), to multiple sized species with stems (C). The packing outcome was very dependent on the random selection at the early iteration stages and was still tending to be increasing when iterations stopped (Table 2).

For models (E-O) of alternating arrival and growth, the model E was taken as possibly the most realistic ecological reference, with the others as the effect of changing single parameters around that reference (Figure 3, Table 2). The packing was least for models where there was no allowable displacement of existing individuals and with packing continuing to decrease at the presentation stage (F-I). The other models were still showing fluctuating packing levels at the presentation stage.

Allowing for an external stem had a relatively large effect on increasing the relative density and packing in most models as might be expected (M cp N; E, K cp H,L; B cp C), but effect on packing was small if there was no allowable displacement (F cp G; I cp J). Shifting the allowable duration of an individual at one size before deletion from a common value (5) for all species and individuals, to it being proportional to its current size resulted in a decreased relative density and slightly higher packing (M cp E), while allowing greater duration for potentially larger species gave similar relative density but lower packing (F,I cp E,K). There was a slightly higher density if the displacement rule was ‘less than’ (O cp E) rather than ‘less than or equal’, as in most models. The shifting of

probability of arrival from being equal for all species to being ten times larger for the smallest species relative to the largest, or visa versa, had relatively little effect (E, P, Q) on density and packing after high number of iterations given at the presentation stage.

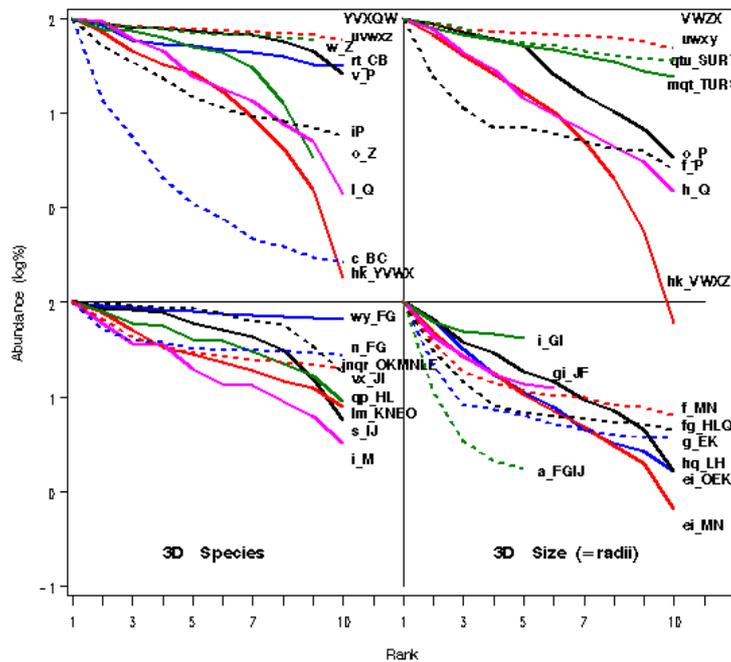


Figure 4. 3D random loose packing SADs. Relationships either as species (left side) or radius sizes (right) and abundance as either density of individuals (----) or as cumulative sphere volume (—). Model coding as in Table 2

The packing values for the self-thinning models were from towards the end of the iterations when there were between fifteen and fifty remaining individuals. For the ten species models (V-Z) there were a wide range of packing levels at that stage, highest where the displacement rule was ‘less than’ (W), and least where there was ‘no’ displacement and where space only became available from the duration parameter. There was a similar trend in the single species models.

3.2 Abundance/Rank Relationships

SAD models (B, C) where individuals of species were inserted at their final size and with no displacement were static models with species and size considerations the same. These gave the largest contrast between the abundance metrics used for the 3D models, and having the steepest and concave gradient using the density metric as compared with the volume metric (Figure 4 – c_BCsd cp rt_BCsv). The cumulative net abundance of the different species was very similar using the volume metric for abundance and no appreciable difference in the relationship if individuals had an external stem.

The model E was taken as the reference model where there was alternating random arrival and random selection for growth and mortality. In the early iteration stages (less than 20 iterations) most species could find space unhindered by the presence of others and most could also make unhindered initial growth. Thus at the early stages there was no pattern (random) in species ranking for abundance, but a limited range in ranking by size, with a steep gradient from dominance in volume by the few individuals that had succeeded to grow. With further iterations that rapidly changed, with further arrivals and possible interaction on growth of those already present from displacement restrictions from other so that the density of individuals became dominated by the smallest sizes and decreased successively for larger sizes. However, a full range of sizes was not achieved until c10K iterations. The mean gradient of the SAD by volume was moderately constant after about a hundred iterations, though slightly steeper and concave earlier, to near linear later. There was an indication that the size ranking order was starting to invert when iterations were stopped.

Models where there was alternate arrival and growth but no displacement (F-J) were partly dynamic and partly neutral in that any other previous species or size could stop potential growth of a selected individual. These had very

similar SAD for different abundance metrics and had shallow gradients. For volume and density there was a trend for the relationship to be slightly concave when allowable duration at one size was similar for all species (wy_FGsv, n_FGsd) with no ordering in relation to species, but slightly convex when allowable duration was proportional to allowable species size (s_IJsv, vx_IJsd) and a trend for the largest to dominate. However considering size independent of species, the main effect of non-displacement was to limit the sizes obtainable by the potentially larger species and a consequent high density of individuals of small sizes, with some interaction between duration and external stems on volume SAD but not size relationships (i_GIrv, gi_JFrv, a_FGIJrd).

Considered as species, seven of the models (E, H, K-O) with the abundance metric density, had similar density SAD of moderate slightly concave gradient. However, there were differences when the volume metric was considered, with a slightly less reduction in the abundance of the first few ranked species when the individuals had an external stem in two instances (qp_HLsv), and a moderate gradient in another (i_Msv).

Considered as individual sizes rather than as species, most of the models in the group had a relatively linear uniform gradient between the fourth and eight ranked sizes and differing in the earlier ranked species. For the volume metric the initial decrease was lesser for two of the models with external stem (hq_LHrv), than for the reference and two other models (ei_OEKrv), and a greater decrease for the tenth ranked size for two models (ei_MNrv) with external stem. Using the density metric, the pattern was nearly reversed.

Two models (P, Q) compared different probabilities of arrival. As species the SAD had a shallow gradient where smaller sized species had higher probability of selection for arrival – lesser for volume than density (v_Psv cp i_psd). Those two models also differed in that intermediate species or sizes dominated the ranking. Where larger potential sizes had greater probability of arrival (h_Qrv) the gradient of the volume SAD was steeper and dominated by the larger sizes. When sizes alone were considered, the gradient of the SAD increased progressively for a higher probability of small sizes arriving to a higher probability of larger sizes arising (o_Prvc cp h_Qrv), and a reverse sequence for the density metric.

The series of self-thinning models had an initial arrival stage of random occupation of a domain by a high number of individuals of zero or small size (radii =1), followed by repeated random selection among those for consideration of growth together with displacement of any surrounding individuals.

The first group of models considered only a single species with possible growth of individuals to a large size (radii = 100) in unit increments. After a high number of iterations there were about thirty sizes. The size SADs were very similar for the four models with both the density and volume metric (qtu_SURTrd, mqt_TURS) with a flat gradient indicating similar contribution by different sizes. In all model the largest size did dominate considering volume but unclear pattern with other metrics. There was minimal effect of allowing an external stem and no displacement gave only a slightly steeper gradient than displacement. The minimum gradients in the SAD was for the linear or area metric.

The second set considered ten species and the individual size limited to their nominal maximum size for each species. All species and sizes were present at the presentation stage.

As for a single species, four of the models (V-Y) were very similar and combined for presentation, with again the model Z, with a high value for the duration parameter, being the exception, though with a less difference between the largest and other species or sizes.

In the SAD the largest dominated as species for all metrics and the SAD gradients steep and convex for volume (hk_YVWXsv). The gradient for the density metric was shallow with a tendency for intermediate species to dominate (uvwxyz_YVXQW). The smallest species was absent from model Z (w_Zsd, o_Zsv). The wide contrast between the single species and ten species model in the density SAD relate to the approximate thirty classes of the former and by only presenting ten ranking with the volume and density metrics represented different ends of a spectrum of radii sizes.

The relationship between density and mean size in the different self-thinning models was investigated in relationship to the proposed $-3/2$ (sic -1.5) thinning rule based on volume/area consideration, or its current contending coefficient of $-4/3$ based on internal distribution network considerations. Regression was applied to the collective data from the different stages of the iteration, excluding the initial stage where there had been a random population of arbitrary small individuals. The relationships for the single species models were linear with gradients ranging from -1.71 to -1.48 and standard error of 0.02 (Table 2). The relationships for the ten species model was slightly convex curvilinear with an average shallower gradients of -1.67 to -1.28 but -1.39 to -0.62 at upper end.

3.3 Size Distributions

In the random packing models where there was alternate arrival, growth, possible displacement and mortality, the

density of individuals were generally increasing as iterations proceeded. However, after several hundred iterations there was no discernable trend in the mean weight, variance, skewness or kurtosis of the collective individuals as iterations continued – just a shift in distribution between different species.

Within the self-thinning group of models where there was a high density of initial propagules with subsequent growth, that as iteration progressed, there was the expected decrease in density with increase in mean size and variance.

Where there was allowable displacement of smaller individuals by larger individuals there was a decrease in kurtosis (distribution became more even). In contrast where there was no allowable displacement, kurtosis was neutral or increased (model Z).

4. Geometric Regular Packing

4.1 Simulation Models

The previous models considered random placement of individuals and their subsequent interactions. A limit-case analogue is where there was regular geometric placement of all individuals.

Mathematical interest and theorems in such regular packing came from the consideration of maximum possible packing of uni-sized circles in 2D and uni-sized spheres in 3D under different regular touching arrangements (e.g. square or triangular packing in 2D through cubic, rhomboid etc. in 3D). From that followed the consequent interest in the allowable sizes and density of circles or spheres that could fit into the intercies between touching larger individuals. Diagrammatic representations of some are presented (Figure 5). In view of the ground touching models described, the figures are better viewed as from a ground surface looking up than from above looking down.

The interest as possible ecological analogues is that such potential packing models would define both the allowable size (radii) of individuals of different species, and their frequencies. However, as ecological assembly analogues, the models are static in that species are inserted at their final size, the size of the largest species determines the allowable size of other species, and that species arrived in rank order.

The simulation models that follow conformed with the condition for 2D models that the outer three circles of the largest species were mutually touching, and for 3D models that the four outer spheres were mutually touching, before the inner circle or sphere radii could be determined from Soddy's theorem (Soddy, 1936) and their coordinates from the Descartes theorem.

A general computer algorithm for size and coordinates was developed for these. An initial relatively coarse grid coordinate system was established for the possible unit space for a particular model, the size and coordinates entered for the largest species, and the grid coordinates that were then not available deleted. Subsequently the remaining coordinates were searched for those that had the maximum available surrounding space as a first approximation of the maximum possible next species size. The estimate was then refined by random search in the proximity of that grid point to give a final estimate of a radii and coordinates to a desired degree of accuracy.

The sample unit was defined as the smallest configuration of area or volume for individuals of the largest species that could be repeated in an infinite pattern. For the sample unit to be part of any infinite design, there was the requirement that any inner sphere either lie entirely within the unit volume or shared exactly equally between adjacent units.

This process of estimation and deletion of possible grid coordinates was continued until 150-200 individuals had been placed. Smaller species were referenced to the radii of the largest (=10). Subsequently packing and SAD were determined for cumulative densities, areas or volumes. Results are given for nine models (Table 3).

4.2 2D Circle Packing (3 × 3 Models)

The three models compare packing to a boundary or square or triangular infinite pattern. While the simple 2D model of a single layer packing to a boundary (B) is an unlikely ecological analogue, it shows several features which are present in many of the regular geometric packing models. The unit is a square which could be repeated infinitely (Table 3, Figure 5 and 6).

In comparing the consequential SAD, the first point to note is that the variations or fluctuations in the presented response lines are a function of the models, not as in the previous stochastic models random statistical, computational or plotting variation. They are actual restraints inherent in the packing structure –that successive sized circles or spheres are not a continuous smooth series. This aspect is present in all of the geometric packing models. In ecological application it would need exceptionally accurate empirical observation sets to detect those fluctuations in possible discrimination between different models and empirical observations.

Table 3. Coding, parameters and 10-species total packing for different 2D and 3D of geometric regular packing models dependent on the touching packing arrangement of the largest

Code	D	Conf	Dom	Lay	Pack	Size	Grad	Size/abundance			
								d	l	a	v
2D with species as touching circles											
B	2		B		98	0.87	1	-	+	+	
S	2	S	I		99	0.56	d	-	+	+	
T	2	S	I		99	0.36	d	-	+	+	
3D with species as touching spheres											
T1	3	T	B	1	8.6	0.91	1	-	?	? +	
S1	3	S	B	1	8.2	1.28	1	-	?	? ++	
S1c	3	S	B	1	15.5	1.89	1	-	?	? +	
T2	3	T	B	2	30.1	1.56	1	-	?	? +	
S2	3	S	B	2	27.2	1.74	1	?	?	+ +	
SI	3	S	S	1	17.3	1.04	1	?	?	u+ u+	
3D with species as ground touching spheres											
T1g	3	T	G	1	14.3	0.74	1	^	-	+ +	
S1g	3	S	G	1	13.4	1.20	1	--	-	+ ++	

D = dimensions (2 = 2D, 3 = 3D). Pack. = packing configuration. (S = square, T = triangular). Dom. = domain. (B = packing to a boundary, I = infinite, G = ground touching 3D). Lay. = number of layers of largest. (1, 2, or I = infinite). Pack = packing after 10 species.

Individuals of identical size can occur in association with different combinations of surrounding sizes. As an analogue this could be interpreted as either two different species having similar ecological amplitude or suitability, or the same species occupying two different ecological niches.

From a mathematical perspective it is noted that many of the sizes of successive ranked species are integer fractions of their radii (= curvature) e.g. for model B: 1/1, 1/4, 1/9, 1/12, 1/16, 1/24, 1/25, 1/25, 1/28 and 1/33.

For model B, similar sizes are noted for the 7th and 8th ranked species among the first ten based on radii. Within the first thirty three species there were similar occurrences at 13th to 15th position (3 species), 19th to 21st position (3 species), and 25th to 27th position (3 species).

After density is considered, the ranking of species for total area (or volume in 3D models) can differ from that of their radii ranking. For model B the ranking of the first twenty species based on radii change to 1, 2, 3, 5, 4, 7, 8, 9, 10, 6, 11, 13, 14, 15, 16, 12, 17, 19, 20 and 21 when based on total area.

There were only small differences in the relationships whether the same sized individuals occupying different surrounding neighbours in the 2D (and 3D models) were regarded as a single or different species. The results presented were for the assumption that they were the same species.

The difference between the three 2D models in the SAD was not great with the density metric, but of a much steeper gradient for the area metric (Figure 6, Table 3). The density of species decreased for successive smaller sizes of the three largest species and was somewhat similar for further species, though with fluctuations relating to the structure of each model. The three largest sizes dominated in terms of total area contribution. While there was a general trend of lesser total area contribution for successively smaller sized species, there were similar fluctuations related to model structure.

The effect of model structure is most apparent in the SAD for density of individuals with conspicuous steps in the graph from the more frequent smaller species to the less frequent larger species (q_B, s_S, s_T).

The SAD for cumulative area is steep and concave for the three 2D models (c_B, c_S, a_T). The gradient is steepest for the triangular packing of the largest circles and with a change of slope at the second ranked species.

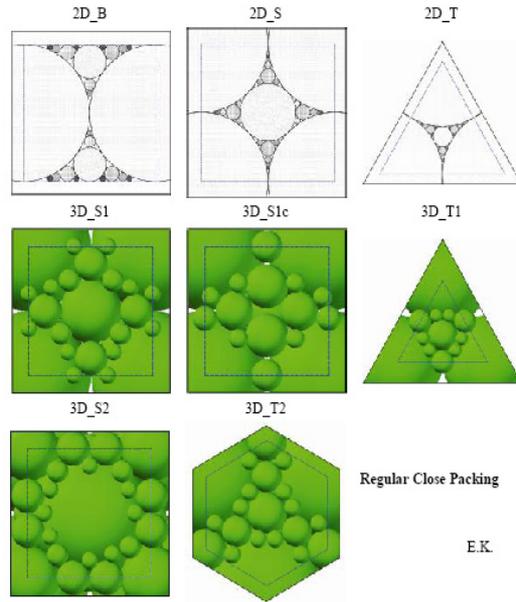


Figure 5. 2D and 3D geometric packing models - diagrammatic representations. 2D species: 2D_B = To a boundary model, 2D_S = square, 2D_T = triangular. 3D bottom surface view of single layer of largest, and species as touching spheres: 3D_S1= Square packing from boundary, 3D_S1c = Square packing from boundary, 2nd in centre, 3D_T1 = Triangular packing to boundary. 3D bottom surface view of double layer of largest: 3D_T2 = Triangular embedded packing and to a boundary, 3D_S2= Square embedded packing and to a boundary

The results are only presented for the first ten largest sized species (= radii). The 2D models were continued out to thirty or so species. In the SAD's these indicated a region of similar relatively-flat uniform gradients from about the tenth to the twenty-fifth species before a possible down-turn to a steeper gradient for further species, suggesting a response curve not unlike a log-normal relationship.

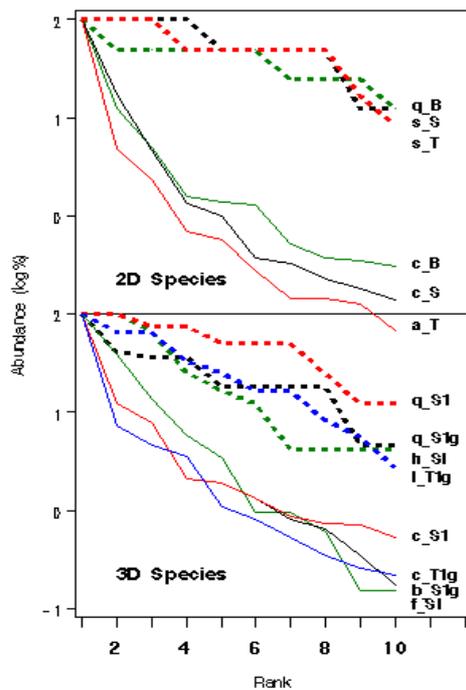


Figure 6. 2D and 3D geometric packing. For ten species (upper) and size (lower). Coding as in Table 3

There was a much greater range in size of successive species (over two orders of magnitude) in these regular packing compared with the arbitrary chosen ten unit increments used in the loose packing models.

The total packing achieved with geometric touching packing models was about double that of the random placement models. The minimum gradient for abundance by size relationships was for the linear metric of product of density by radii.

4.3 3D Sphere Packing (8×4 Models)

The eight 3D models had similarity in their SADs with either the density or area metric and results are only presented for four contrasting models which had a steep concave gradient for the volume metric (Figure 6, Table 3). The divergence between models was slightly greater considering the density metric SADs.

The range of species sizes (=radii) within the first ten species was less than for the 2D models. The three largest sized species had the greatest abundance in terms of cumulative volume and least in density. Lesser sized species generally had similar frequencies but decreasing contribution to volume, though with many fluctuations related to particular model packing restrictions. The density of species was greatest for the smaller size for the single layer triangular packing mode (T1g), and at successive larger sizes for square-packing single-layer ground-touching (S1g), and infinite packing (SI) models.

The volume/area packing achieved for the two 3D ground touching models was 6.7 and 9.8 respectively for the square and triangular packing. The minimum gradient for abundance by size relationships was generally for the linear metric of the product of density by radii.

5. What Is a Specie's Abundance

The feature that the simulation studies emphasize, because of the ease with which parameters can be changed, is that the form of the SAD is very dependent on which metric is used for 'abundance'. In empirical observations that may relate to the characteristics of an individual of a species such as presence/absence, size (radii), area, volume, or mass; but more usually the cumulative total for all individuals of a species as density, cumulative area, volume, mass or some other metric of the product of density by size (e.g. extent of distribution network, or metabolic mass).

This is illustrated in Figure 7 for ten species with unit decreases of radii as used in the random loose packing models and assumed to have equal density. With equal densities the SAD are the same whether consider individual or cumulative characteristic of a species are considered. The SAD for individual characteristics has the same features of supposedly cumulative abundance distributions. They are convex, the largest species always the most abundant, retain the size sequence, and gradient increasingly steeper as the parameter changes from density through area to volume, and cover a similar range in values. Comparison of these responses with the likes of the 3D loose random packing models (Figure 4) show that the gradients are generally shallower in the latter, indicating more equal distribution between species in cumulative total.

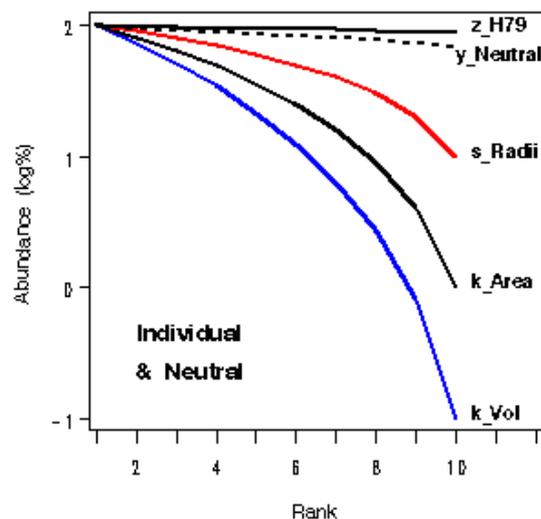


Figure 7. SADs for ten species of equal density in unit decreases of radii and expressed as either individual or cumulative abundance as area or volume (Radii, Area, Vol). Also combined neutral theory models (Neutral, H79)

The issue has less to do with model construction, but becomes crucial in considering the wide range of methods used to obtain abundance estimates in empirical ecological observations and the subsequent stages of deciding which may be the most appropriate models to compare them with. For example many of the neutral theory models have the implicit assumption that abundance is the number (density) of individuals of a species irrespective of any difference in size between individuals or species.

6. Random Loose Packing with Differing Size Decreases

6.1 Simulation

The initial set of packing models used an arbitrary selection of potential maximum species size as uniform decrease in potential species sizes with models differing in their growth and displacement parameters. They also concentrated on the implication of the differing resulting densities and metric used for the SAD.

Those relationships tended to have a convex curvature (Figures 2, 4, 7). By contrast the geometric regular packing models, where the model requirements defined both the size and density of different species, showed both a rapidly decreasing size of successive species and a tendency towards concave curvature in the resulting SAD (Figure 6). This suggested that the form of the differences in potential relative size of species could be as important as their resulting densities in determining the SAD. The following simulations used the same program as above for 3D loose packing models but differed in the assumed potential size of the ten species.

Nine of the models used potential radii from the regular packing models and three were for species with successive potential radii in geometric series size for $k = 0.3, 0.5, \text{ and } 0.7$ and. The other parameters were as for the reference model of alternate arrival and growth, no external stem and displacement if surrounding individual were less than or equal to the potential size of the growing individual. As the general simulation program had been designed using integer increments this further set of simulations had the largest potential species set to a radii = 100, with other species radii rounded to the nearest integer of the corresponding model, the total sampling area increased to a 1000×1000 grid and simulations continued for forty thousand iterations. The reference model was also repeated the larger scale.

6.2 Abundance / Rank Relationships

The change of scale and retaining integer increments meant that the relative increments were smaller with a greater possibility of different radii sizes and probably greater effect of duration before mortality. Consequently the models with the same computing time did not progress to the same level as earlier models and probably not directly comparable with them. Computing resources were not available to take the iterations further. However, the models did have features of note. The modelled decreases in potential species sizes were all greater than the uniform decreases used in the previous models. In all models the larger species had only reached a fraction of their potential sizes with only 1-3% of individuals exceeding a radius of ten compared to their potential of a hundred. The SADs were very similar for all nine models.

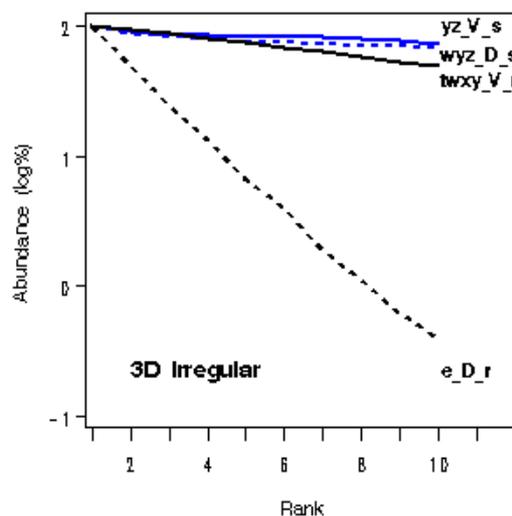


Figure 8. 3D models with irregular size decreases. V_s = volume by species, D_s = density by species, V_r = volume by size, and D_r = density by size.

The main feature was the very strong log/linear relationship between density and rank with rank progressing uniformly from individuals of the smallest to larger sizes (Figure 8 – e_D_r).

The second feature was the very flat relationship using the volume metric as either species or sizes or densities as sizes (yz_V_s, wyz_D_s, twxy_V_r). The preponderance of individuals of small size meant that total packing was low relative to previous models.

7. Entity Models

The particle packing models suggested above worked from the basis of placement of individual of a species; their frequency of arrival; initial size, growth and mortality; and interaction and displacement with other individuals.

Most of the existing models of community formation consider each species as an entity (cumulative total) and the proportional contribution different species make to that total under different scenarios of community formation (Wilson, 1999). Which abundance metric is used is not implicit in those models, only the proportional distribution between species.

One class are those has some general mathematical form of the supposed random processes involved but having parameters that have to be estimated from the empirical observations at hand. These include the geometric series, truncated log normal and the log series.

Another class are statistical, based on the scenario of differing probabilities of species as an entity arriving into a domain under differing scenarios of interaction between species (assembly and dismantling models). The models are statistical in that comparison with a particular set of empirical observations can only be with the mean of outcomes of a large number of simulations of the assumed probabilistic interactions.

These are considered as assembly models. Some examples are given, both for comparison with the particle packing models and for comparison with some proposed dismantling models of species departing from a community, or taxa models where the identity of species is retained through different assembly and dismantling stages.

Some prominence is given to the geometric series model as a reference for comparing the different models. The attraction of the geometric series model is its simplicity, that it generally gives a reasonable to good description of empirical observations – at least for the more abundant species, has only a single parameter, the relationship can be fitted directly to empirical observations, and for field use the parameter can be estimated directly from either the proportion of the most abundant species, or from the ratio of abundances of any two ranked species.

The concept of the geometric series model (GS) for species colonizing a site is of a first species supposedly pre-empting some fraction $(1-k)$ of a total niche, a second species a fraction k of the remaining niche, the third species the same fraction of the remainder, etc. for a finite or infinite number of different species. The ecological interpretation would be of species already having some order of decreasing suitability for an environment or domain, but until recently, no functional suggestion of why the proportional reduction should be the same for all successive species.

In the application of the geometric series, authors have differed in the definition of the accompanying single coefficient (k). Some have defined it as the fractional contribution of the first ranked species (e.g. Whittaker, 1972; Tokeshi, 1990), while others have defined it as the fractional reduction between subsequent successively ranked species (e.g. Loehle, 2006). The present work used the later definition as fractional reduction between successively ranked species.

For the geometric series the proportional contribution (P_i) of the i th ranked species is - in programming notation:

$$P_i = (1-k)^*k^{**}(i-1) \quad \text{if infinite number of species}$$

or

$$P_i = (1-k)^*k^{**}(i-1) / (1-k^{**}n) \quad \text{if finite number (n) of species}$$

The geometric series model is fixed for a particular value of k and the number of species.

Two other models with coefficients determined from empirical observations are the truncated log normal (Preston, 1948) and the log series (Loehle, 2006).

There are a number of conceptual and mathematical considerations illustrated by the geometric series and the other assembly and dismantling models to be discussed.

The first is that species ('rank species') are defined by their rank order of abundance or proportion within a group of species, is independent of what was the identity of those units in any previous or subsequent species group size, and is retrospective. This 'rank species' concept is implicit in the geometric series model, and also in most other models

to be presented - following re-ranking of components after determination of proportions at each stage.

The retrospective determination of rank from abundance will mean there will always be a high negative correlation between abundance and rank. This applies to both the hypothesized expected model values, and empirical observations.

There will be some consideration of possible models where the identity of species ('taxa species') is retained in random assembly and dismantling processes and their ranking only determined at a presentation stage.

8. Assembly Models

8.1 Simulation

Tokeshi (1990) has reviewed a number of different assembly models as a domain is subdivided by successive contributing species, together with their possible ecological analogue. The following is partly a paraphrasing from his work.

Dominant pre-emptive (DE): In the assembly rule for this model, while still implying a rank order of suitability for successive species as in the geometric series, it differs in not assuming that the proportional reduction is constant - only that it is some random uniform fraction greater than 0.5 at each successive partitioning. The ecological analogue is of retaining the concept of a decreasing rank order of suitability, but that the reduction factor can be variable.

Random fraction (RF): This model envisages niche apportionment as a sequential division of a total niche in a random fashion. The niche is first divided in a random uniform manner into two fractions; one of which is then randomly selected for further subdivision in a random uniform fashion; and continued in a like manner for the number of species considered. The species are then re-ordered according to their relative abundance. The ecological analogue would be of a new species invading the domain of existing species, the selection of the species to be invaded being random, but invasion subsequently confined to that species domain.

Broken-stick or MacArthur (BS): The random fraction model assumed that all species niches at one stage have equal probability for selection at the next sequential division stage. Tokeshi (1990) showed that the broken-stick model can be generated in a similar manner if the assumption is moved from equal probability, to the probability for domain to be selected for subdivision as proportional to their existing proportions, though not influencing the manner of its subdivision. The ecological analogue is for there to be some propensity (but no explanation other than neutrality) for the domain of a species to be preferentially invaded by a new species according to its abundance, though with the invasion then confined to that domain.

Dominant decay (DD): The possible propensity for the domain of the most abundant species to be divided is taken a stage further in the dominance decay model. In it the species with the maximum proportion is selected for subdivision at each stage, though with subsequent subdivision in a random uniform manner. There is no obvious ecological analogue of why this might occur - other than as a host specific pest or disease, or selective removal of the dominant e.g. logging)

Random assortment (RA): The simplest model is that of communities being just a random assortment of species modelled as initial random uniform probabilities for each species for a particular group size, and then their the relative contributions ranked. Note that in this model the proportion of a particular species at one group size is not related to that in another group size. The ecological analogue is for a sparse occupation of a new domain, or no interaction between species, or a fluctuating environment where there was changing suitability between species.

New arrival (NA): A further model is added in the present work which simulates a new arrival into a community of already established proportions of previous species. The effect is either increasing the total that has to be proportioned, or relatively proportional capture of all of the other species previous domains. It was modelled as random uniform estimates of proportions of species at one group size scaled to unity, then a random uniform estimate for a new species at the next group size added and all re-scaled back to proportions.

All the assembly models are statistical. For comparison with empirical observations the comparison has to be with the mean of a large number of simulations for each of the different models. In the present work the stochastic response function used for each of the models was the mean of a thousand simulations using a random uniform function (SAS uniform (0)) for the random component, and taken to a total of 20 species. Results are given for the ten most abundant species in each model (Figure 9).

8.2 Abundance /Rank Relationship (6 Models)

The relationships between relative abundance and rank is only strictly linear for the geometric series models (Figure 1-b_0.20, b_0.32, e_0.50, l_0.70) but essentially linear but slightly convex for all other models, at least for the ten more abundant species.

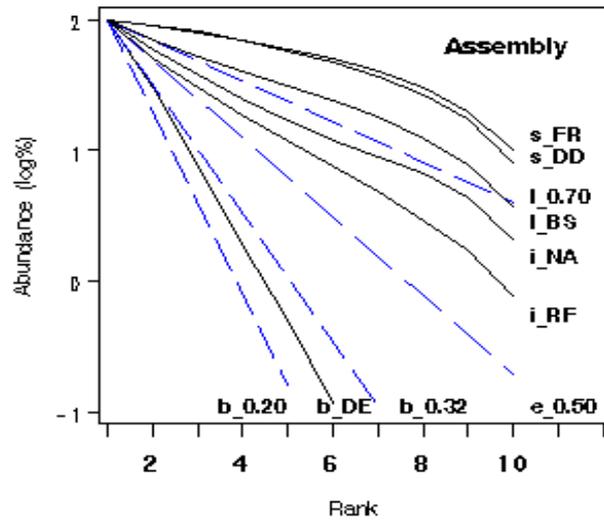


Figure 9. Assembly model SADs compared to the geometric series. FR = Full random, DD = Dominance decay, BS = Broken stick, NA = New arrival, RF = Random fraction, DE = Dominant pre-emptive

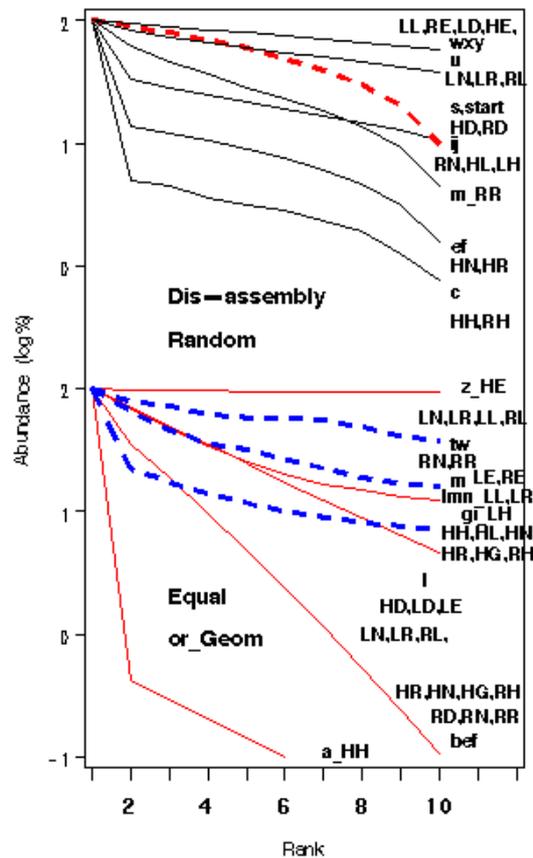


Figure 10. Dismantling models SADs for assuming random (R), equal (E) or geometric series ($k=0.32$) (G) starting fractions for 20 species. 1st coding letter – species selected for deletion at each stage (H = highest, most abundant species, R = random selection from species, L = lowest, least abundant species). 2nd coding letter – species to which released domain assigned to (D = simple deletion, H = assigned to highest remaining abundant species, N = to next most abundant species to that of deleted, R = random allocation to remaining species, L = to lowest species, E = divided equally among all species)

The dominant pre-emptive model (b_DE) is near linear with a steep gradient. Other models tend to be slightly

sigmoid (i_{RF} , i_{NA} , l_{BS}) or convex and of shallow gradient (s_{DD} , s_{FR}) within the range of the first ten ranked species. The mean of simulations for the dominant pre-emptive model (b_{DE}) gives a similar decrease to that of the geometric series without assuming the proportional reduction between successive species is constant. What is not shown by the figure is, that except for the geometric series and dominant pre-emptive model, is that the relative proportions of a given species changes depending on the total number of species considered.

9. Dismantling Models

9.1 Simulation

The possible explanation of the ecological analogue of the different assembly models depends on a scenario of a domain being successively colonized by a range of species and in the order of their final dominance. But an alternative is of a group of species being already established and some change in conditions leading to their thinning or mortality. That would be dismantling rather than assembly and consideration is given to an equivalent class of dismantling models.

There were three aspects of the different models considered: what were the assumed starting proportions of different species? Which ranked species was selected for deletion or amalgamation? and which of the other ranked species was any released domain added too?

The assumed starting proportions were either equal for all species (E), or random proportions (R), or of geometric series proportions (G) (for $k = 0.32$). As an ecological analogue the first was unlikely but used as a reference, the second a guestimate in the absence of specific information, and the third to simulate a value close to empirical grassland data.

The species selected for deletion were either that with the lowest proportion (L), a random selection among all species (R), or that with the highest proportion (H). As an ecological analogue the first was the most likely as a deletion of the least suitable species, the second a guestimate in the absence of specific information, and the third unlikely (short of selective harvesting).

The released domain was either deleted (D) (which is equivalent to sharing it proportionally with remaining species), or randomly allocated (R) to another species, or allocated to the species with the highest proportion (H), or allocated to the species of next highest proportions to that deleted (N), or subdivided in equal (E) proportions between remaining species. As an ecological analogue the first was the most reasonable, the second a guestimate in the absence of specific information, the other two as further capture by the dominant species or by the species of adjacent better suitability to that deleted, and the last unlikely.

The factorial combination of the different options led to a large number of alternative models with simulations starting with 20 species, uniform random function and made for at least a thousand iterations.

9.2 Abundance /Rank Relationships

Models with random starting proportions at the top of the figure show increased in similarity of proportion between species relative to starting proportions (Figure 10 –s_start). Most were for where the lowest ranked (L) species was selected and re-assigned to the lowest (L) or equally (E) between remaining species (wxy_LL,RE,LD,HE, u_LN,LR,RL).

Several of the models with random initial proportions showed a break in slope at the second ranked species with a convexity over remaining ranks.

Those were mostly from models where the largest was selected and the released domain added to the highest (H) or next highest (N) and reflect an increased dominance of the first ranked species ($c_{HH,RH}$, $ef_{Hn,HR}$, $s_{HD,RD}$) The break of slope is of interest in that it may give an explanation of why in empirical observations the proportion for the first ranked species often seem to be disproportionately higher than a smooth continuous series.

The assumption of equal starting proportions, while ecologically unlikely, does indicate some boundary conditions (Figure 10 lower). The decrease in proportion through successive ranks is relatively small for most models – least when the lowest rank species was selected ($tw_{LN,LR,LL,RL}$) and increasing as the first ranked species was selected ($gi_{HH,HL,HN,HR,HG,RH,LH}$).

The using of an assumed geometric series starting proportions was strongly maintained in most subsequent dismantling models. The exception were some combinations where the lowest was selected ($l_{mn}_{LL,LR,LE,RE}$) giving slightly more even in proportions, and the increasing dominance of the first where the highest was selected and reallocated to the highest (a_{HH}).

Five of the dismantling models showed some maintenance of equality in proportions from the second rank on. With the re-ranking of species after each step in the model iteration, the net effect of many of the model permutations is to add released domains to that of the increasingly dominant species as noted above. In similar allied simulation models undertaken, the difference in proportions between the first and other species increased as the assumed starting number of species increased.

10. Assembly /Dismantling Models – Taxa Species

10.1 Simulation

The assembly and dismantling models described above are retrospective models, in describing what may have been the past influences that have created the present observed proportions, and in several instances using the wisdom of hind-sight of knowing the final rank order or suitability of species. They also tend to be large scale, static, and do not allow for the species to be growing or declining while new species are added or species removed.

As a possible analogue of ecological processes the least satisfactory aspect of those models is that the identity of a unit can change between successive steps in a model simulation. The identity of a species is defined by its rank order within the other units present at each stage e.g. what may be classed as the 5th ranked species at one stage and representing a particular taxa grass species, may be re-classified as the 8th ranked species at the next stages which previously had been a particular herb taxa species. An alternative class of partial dynamic models were investigated where the unit was retained as a taxa species, various random additions or deletions were made to each taxa species total pool, with their relative rankings only determined at a final presentation stage. As a partial dynamic model, the models also considered growth of existing pools as well as random additions or deletions.

The five aspects of the different models were the number of potential species; whether an assembly (A) or dismantling (D) model; the starting total for each species (zero for assembly models); the random element of species selected and amount added (for assembly models) or deleted (for dismantling models to zero); relative growth rate of different existing species either equal (E) or random (R) (but remaining fixed within each iteration run); and multiplication of these within one iteration period (1 = no growth, 2 = doubling of previous pool size in one iteration period). The models are again statistical and the results are the mean of at least a 1000 iterations for each species group size. The models used random uniform in the range 0-1, to represent species contribution and initial random uniform to give relative suitability of different species multiplied by a common factor to give either net growth or decrease.

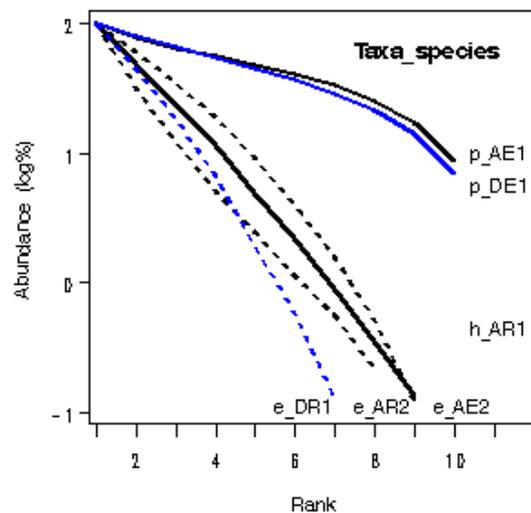


Figure 11. Taxa species SADs for eight assembly and dismantling models where identity of species is retained through iterations 1st coding letter – model type (A = assembly, D = dismantling). 2nd coding letter – starting growth rates (E = equal, R = random). 3rd coding number – growth or multiplication factor of species in unit interval (1, 2)

11. Neutral Models

11.1 Simulation

Implicit in the above classes of models is some form of difference in suitabilities or competitive interaction between species. In the past decade there has been investigation of another class of neutral theory models which question whether those assumptions are necessary.

The neutral theory set of community composition models start from the assumption that all individuals within a local community in a given environment are competitively equal irrespective of the species involved and that many of the features of species composition just come from random drift. The scenario is that starting from a closed community of a fixed number of identical individuals, that changes in composition over a periods come from the chance death of an individual and its replacement by a similar individual, or a mutant as a new species (long time scale), or the colonisation by an individual of same or another species from an outer meta-community (short time scale). The concept is at variance with other genetic and ecological concepts such as speciation, adaptation, niche, competition etc., but in practices provides a similar fit to empirical observations as other models. Consideration of the current state of understanding of these models is given in Chave (2004), McGill et al. (2006) and Holyoak et al. (2006) and associated papers in those assessments.

In relation to the other models considered they are assembly models in starting from a single species or a group of identical species; stochastic in the sense of either mutation rate or invasion rate with state at any stage related to the previous state; dynamic in that composition changes through time and only stabilizing after a long period in a statistical sense. They differ in the concept of starting from a closed community of a fixed number of individuals, rather than individuals or species colonizing a new site. They also consider only the presence of a species (frequency or density) without any reference to a metric for the size of an individual. Also, as in most other models, the ranking of species is retrospective.

The present simulations considered four of the ten type types of neutral models outlined by Chave (2002 – Figure 2), Chave et al. (2006) and McGill et al. (2006). As the present interest was in SADs, and to make comparison with the other models, consideration was limited to models for ten species. A closed starting local population of 10 000 individuals randomly allocated to ten species in equal proportions was used. Following that, through a number of iterations, was the random selection of an individual; consideration of whether it was deleted, remained the same, or increased; its replacement or addition from a surrounding meta-population; and also how the meta-population was also changing. The local population was treated as a sample of a larger spatially implicit meta-population under similar conditions and trends. The species proportions in the local population were determined after each thousand iterations, the meta-population then changed to mimic those proportions, repeated for 100 such further stages, and replicated 5 times from similar equal starting proportions. ‘Random’ was used as meaning random uniform throughout.

H79: In the first model (from Hubbell, 1979) there was random selection of an individual for deletion and the reoccupation by a random selection of an individual from a surrounding meta-population of the same species in equal proportions (as if a local population was subjected to a constant seed-rain from a surrounding population of constant equal proportions).

H01: A further modification in the model (from Hubbell, 2001) was for the meta-population to also be changing in species composition in relation to some global changes. This was simulated by the meta-population being changed to mimic the species proportions in the local population after each thousand iterations.

To be more correct the meta-population should have been much larger than the local population. The effect of making the meta-population similar to the local population after each 1000 iterations in this and the subsequent three models meant in effect modelling only neutral models in a local population without the stabilizing or dampening effect of a larger meta-population. The approach was felt justified in more rapidly determining the effect of drift in local species proportions.

Ba: Bell’s (2000) model considered both the possible reproduction or loss of an individual as well as a new arrival from the meta-population. This was simulated as the random selection of an individual, random decision on whether its potential of growth was greater than its replacement – with growth meaning an increase in density of that species by one, and random selection for addition of an individual from the meta-population. Where there was both the increase of an existing individual and an arrival of a new individual from the meta-population, there was the need to arbitrary randomly delete two individuals from the local population to maintain the assumption of constant size. The model continued with the assumption that the meta-population would continue to change mimicking the changes in the local population.

Bb: Similar to the previous with the difference that an individual could be deleted, remain, or increase by one for the corresponding thirds of a uniform random function.

C: In the above four models the location of an individual within the local population is not considered. Chave's model (2002) considered that any replacement of an individual within a local population is more likely to come from species in the immediate vicinity (as in local self-seeding) rather than from some distant meta-population.

This was simulated as the individuals being in a 100x100 grid and in the manner of the Bell model above of the random selection of an individual, random decision on whether its potential of growth was greater than its replacement- with the difference that any replacement was a random selection of a species similar to that in the eight surrounding positions, while the selection of a new arrival was from the meta-population. The model continued with the assumption that the meta-population would continue to change mimicking the net changes in the local population after each thousand iterations.

11.2 Abundance /Rank Relationships (5 Models)

Relative to other models all five neutral models, as modelled, gave a very shallow mean gradient of the log SAD; a high coefficient of variation between iteration runs; with all having the tenth ranked species with a relative abundance of c 90% within the first thousand iterations.

The values for the earlier Hubbell model (Figure 7 -z_H79) continued to fluctuate around that level, as would be anticipated from the meta-population remaining constant. Where the meta-population was also changing (H01) there was a gradual increase in the difference between species, with sequences of fluctuating trends within runs due to statistical drift, but not synchronous between runs.

The other three models (Ba, Bb, C) also had a similar gradual increase in difference between species, fluctuations, difference between runs and large coefficient of variation after a hundred runs so that collectively it would be difficult to discriminate between the four in relation to empirical observations.

12. Neutral /Empirical Models

All of the above models carry some implications of a supposed functional reason in the selection processes involved. Most are probabilistic in nature and develop the proportioning or parameters only from the mean from a number of simulations without reference to a particular empirical observation at hand. By contrast the alternative forms of the geometric series and lognormal relationship only define the form of the relationship with some parameters derived from fitting to each empirical observation. In that sense they are partly neutral. They were fitted to all of the empirical observations for both the finite and infinite form of the geometric series and either for only the first five ranked species or for all available ranked species.

An alternative was not to imply any selection process and just fit a descriptive polynomial to the SAD of each empirical observation. This was done using a quadratic relationship with fitting only appropriate for the logarithm for the first ten ranked proportions.

$$\text{Log}_{10}(\text{Abundance}) = 2 + a * (\text{rank} - 1) + b * (\text{rank} - 1) ** 2$$

13. Comparison between Models

The relationship between the different models was compared based on the first two axes of a principal components using the second to tenth ranked proportions, the *k* coefficient of the geometric series fitted to the first five ranked proportions, and the *a* and *b* coefficients of quadratic fit to each model. The particle packing models included density, linear, area and volume configurations of each model.

There was grouping of some of the models types within the general scattergram (Figure 12A). The two regular 2D or 3D packing models on upper left with models based on cumulative volume in the upper left edge, grading through area and density metrics to linear toward lower right margin of group. The 2D regular models are on the extreme left and 3D models lower and from left to centre.

By contrast the neutral models with relatively similar abundance of all species are part of the group of models on the upper right edge

The assembly models form a linear group through the lower edge of the scattergram from the 'dominant pre-emptive models on the left through 'random fraction', 'new arrival', 'broken stick', 'dominant decay' to 'fully random' on the right. Some of the taxa models form the lower left extremes. The other model types had representatives dispersed throughout the scattergram.

For the 2D and 3D models with uniform decreases in potential species size, those models with insertion of individuals at their final size are in the upper left extreme section. Models based on density were predominant on

the left and only a weak trend towards change to linear, area or volume metrics towards the right. With the 3D models there was trend for models based on size of individuals to predominate on the left through to those based on species on the right.

The 3D models with differing decrease in potential size were concentrated in the lower right section of the scattergram. They showed a strong trend from differing individual's size on the left through to those based on species on the right, and from models based on metric of density through linear, area and volume.

The dismantling group of models were dispersed throughout the scattergram. Though potentially there were a high number of models related to different combination of parameters, many of them gave effectively similar outcomes.

The resulting SADs were very similar for different groups of models. The models and relationships were averaged for different sectors of the scattergram and were the basis for the retrospective coding of models (Figure 12C). There were 7 to 44 models in each group with greatest concentration in groups i, l, m and w and commonly included a range of model types. The differences within and between some of the mean SADs of some groups were small (see inserts) considering both the actual mean values and the stochastic variability of component simulations.

14. Comparison between Models and Empirical

As indicated earlier, because a species rank has generally been determined retrospectively from its abundance based on whatever metric of abundance was used, that retrospective action alone will always result in a high negative correlation between relative abundance and rank for that procedural reason alone. This is extended further when comparison is made between different models or between models and empirical values where there was retrospective ranking within both value sets. As an ecological interpretation of the relationship between models and empirical observations, this has probably lulled us into a false sense of the invariance of the relationship. The question should probably rather be: what are the possible functional reasons for the particular shape and gradient of the negative relationship for the particular abundance measurement used? - rather than the negative correlation per se.

Two metadata sets of empirical vegetation composition observations were assembled. The first was 432 observation sets containing at least ten species (Table 4). These were 230 from New Zealand Journal of Ecology Vols 1- 30 (various measures); 58 from Rothamsted Park Grass plots (above-ground biomass – Williams, 1978); 52 from various New Zealand vegetations (various (Wardle, 1991)); others from personal sources; 48 from alpine tundra (above-ground biomass (Scott & Billings, 1963)); 12 from subalpine shrubland/grassland (height-frequency = volume (Scott, 1965, 1977)); 32 from tussock grasslands (cover (Scott et al., 1988)). The second was 110 observation containing 5 species and used earlier investigating the SADs in improved grazed pasture composition (Scott, 2006). The two sets were combined for comparison with the models.

Observations in the first set were categorized according to the metric used for abundance of which 30% were as biomass, 12% as vegetation ground cover, 13% as density of individuals, 14% as 'frequency' of individuals equivalent to density, 28% as 'frequency' representing 'presence' within sub-samples of specified sizes, and 3% uncategorized.

'Frequency' or 'density' of individuals is relatively un-ambiguous for animals or single stemmed plant species like trees, but can be very ambiguous for vegetative reproducing plant species. "Frequency" can be particularly ambiguous. It can be equivalent to density, but often just refers to the cumulative presence of a species within a number of samples of specified or un-specified sample size and can includes parts of one or several individuals. The meaning of 'area' or 'volume' can be ambiguous applied to the open architecture of plant species in vegetation, as too whether they are strictly confined to the physical tissue, or to the wider application of dimensions defined by their perimeter as in 'size', 'height', 'canopy spread', 'canopy volume'. There is the similar ambiguity in plant 'cover' especially where single or multiple hits are allowed at each sampling point.

Table 4. Mean and standard deviation of relative percentage abundance at successive lower ranks in the 10-species empirical data set (n = 432)

	Rank									
	1	2	3	4	5	6	7	8	9	10
Mean	100	66	49	38	30	25	21	17	15	12
STD	0	25	25	23	21	20	19	17	16	15

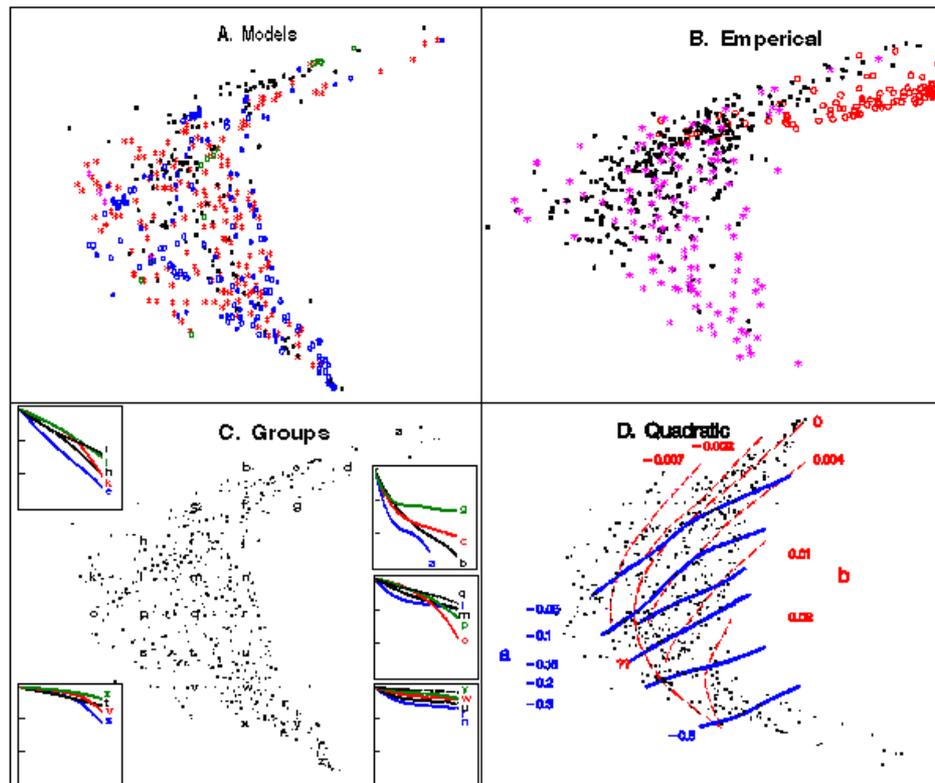


Figure 12. Scattergrams of models and empirical observations based on first and second principal components for model data. A. Models 2D geometric packing (red), 3D geometric (green), assembly (blue, neutral (blue) and others (black). B. Empirical 5 ranked pasture observations (red), 'frequency' as presence in samples (magenta) and others (black). C. Model groups and examples of abundance/rank relationships. D. Isopleths for coefficients of quadratic functions to models

Cumulative biomass measurements (e.g. fresh weight, dry weight, above ground biomass) are relatively un-ambiguous, but no models of SADs have offered approaches directly from that perspective. Those measures probably correlate with volume and would scale similarly for partitioning of biomass between 'canopy' and 'stem' if the ratios were similar for all species, but could be biased if they were different. The scattergram of dispersion of empirical observations on the same coordinate system as the models shows a similar wide dispersion and little clumping of observations (Figure 4B). There was some difference in distribution of values from the second set of observations having only five ranked species and those mostly from developed pastures.

There was a trend of higher frequency of observations in the lower section of the scattergram of having a more equal contribution of different species where the metric was 'frequency' meaning presence of species within samples. That trend would be expected as sample dimensions approaches spatial variability dimensions (if sample dimension were greater than spatial variability dimension then all species = 100% presence).

The question of the 'best' model(s) was approached at three levels: firstly which models gave the best average fit across all empirical observations; or secondly were there better fitting groups of models to different sections of the empirical observations; or thirdly using other criteria for initial selecting the model type to be considered. The wide dispersion in the empirical observation suggests the first is unlikely.

The test of fit between each of the empirical observations and each of the models initially used the two parameters: the sum of square deviation (variance); or the chi-square deviation. Because of the ranking, the former would place more emphasis on the correspondence with the earlier ranks, whereas the later would place more emphasis on correspondence with later ranks. There was no major difference between the ranking of the models or the model groupings using the two different fit parameters and the results are only presented using the variance.

Table 5. Frequency of occurrence of models giving within the three 'best-fits' (Three) or within the ten 'best-fits' (Ten) from 542 sets of empirical observations based on the variance (for r2-r10). Model groups with coding transferred back to earlier corresponding sections

Three best fits			Ten best fits			
(a) Models with individual fitted coefficients						
132	Quadratic		282			
60	GS10_i		190			
68	GS5_i		145			
63	Gs5_f		144			
18	Gs10_f		94			
8	Lognormal		65			
(b) Model groups – layout as in Figure 12						
			6	20		
9 13 31			67 39 70			
37 43 24			150 123 67			
34 72 60			200 204 156			
36 24 29 35			131 175 199 103			
29 22 21 17			92 124 120 72			
11			60 93 74			
6			59 65			
8 3			37 33			
3			18			

The models were separated into classes for the different sectors of the model scattergram (Figure 12C). The goodness-of-fit between the different models or model groups for each empirical observation were ranked. Subsequently the frequency of each model group being within the 'three best-fit' or within the 'ten best-fits' were determined collectively across all empirical observations.

As would be expected, the highest frequencies were for the six models which had all or some parameters derived from each empirical observation (Table 5). The highest was from a direct fit quadratic to the first ten ranked proportions with no implications of the selection processes involved. Even that model was only within the "three best" fits in about a quarter of the 542 sets of empirical observations. The confining of the response to a quadratic polynomial was not sufficient to cover the curvature of many of the SAD's and would be invalid for extrapolation beyond the number of species on which each was based.

Within the four geometric series model alternatives the two infinite series models gave slightly better general fit, with the finite series for five species similar, but lower for a ten species finite series. The log normal was the least satisfactory of the individual fit models.

Those six models with individual fit parameters were then excluded and fit of other models or model groups for each empirical observations re-ranked. However, the other models did include geometric series and log normal model alternatives with constants fixed across all observations.

The discrimination between the better fitting models across all observations was not great with only an 8% reduction in the variance across the best twenty models.

Four of the best models across all the empirical observations were particle packing models of ground touching spheres of uniform decrease in potential species size, initial insertion, growth and limitation on duration at one size before mortality and with all sizes present. Two were 10-species self thinning models differing in allowable duration at one size before mortality but with the relationship with individual's size rather than species

Table 6. Comparative frequency of best-fit between empirical measurements and particle packing models using different abundance metrics and individuals expressed as either species or size (= radii)

Model	As species		As size		Both	
	Three	Ten	Three	Ten	Three	Ten
2D	Random with growth (10)				Regular (3)	
Density	39	95	41	134	7	20
Linear	43	104	45	148	34	82
Area	24	84	67	191	2	11
3D	Random with growth (20)				Regular (6)	
Density	38	201	43	174	47	100
Linear	38	135	79	251	20	62
Area	47	152	91	337	58	165
Volume	67	273	120	380	15	40

designation and with the linear metric (Figure 4 mXrl, Figure 4 lWr1). The other two were with species, either as a higher frequency of arrival of smaller species (Figure 4 mPsl), or one where individuals had stem with duration at one size before mortality determined by current size (Fig 4 lNsv).

However, the other two best-fitting models had a highly random component of being MacArthur broken-stick assembly model (Figure 1 l_MS) and the dismantling model of random initial proportions, random selection and random reallocation of released domain (Figure 2 m_RR). The geometric series model with fixed coefficients across all observations was about the twentieth best-fitting with a coefficient $k=0.74$. The best-fitting of the geometric regular packing models was the two layer triangular packing model at about the fortieth best-fitting model across all observations (Figure 6 q_S2sl).

The second approach was to determine whether there were better fitting groups of models for different sections of the empirical observations. Each model group gave best-fit to some sectors of the empirical observations (Table 6).

The highest frequency of best-fits were with models in Groups h, i, l and m, which also had the higher number of models included (15, 44, 39 and 33 respectively). Within those groups most were particle packing models, with dismantling or assembly models at the lower end of the frequency range.

Those for the geometric regular packing models which define both the density and size of species, were for the 2D model

s those involved with the linear metric (D2b, D2s, D2t)), while those for 3D models were with density, linear or area (D3t1_va, D3t1g_vf, D3t1g_va D3s1g_va Des1g_sf, D3s1c_va)

Within the random packing models most were with individual's size rather than species designation, with those in the 2D models having the metric density, linear or area, and those in the 3D models with area of volume.

Within Group h were seven 10-species self-thinning models with four relating to individuals radii and cumulative volume (h_WXYZrv).

Four assembly models were within the four groups (RF, NA, BS). The four groups also contained two of the dismantling models for random initial proportions, random selection, and either random allocation or allocation to the next most abundant species (i_RN, m_RR) but none of the other random initial proportions models. There were twelve of the dismantling models in Group l of which six were with species starting proportions in a geometric series. Group w contained 46 different models but was only relevant to a small sector of the empirical observations.

Collectively across the geometric regular models and particle packing models with uniform decrease in potential species size, those based on individuals size (= radii) are more frequently better-fits than those based on species identity (Table 5). Species and size frequencies are synonymous for the geometric regular and random growth models where individuals are inserted at their final size.

The modelling was based on packing of area in 2D and volume in 3D and consequent density. The better fitting models did not necessarily follow those metrics. For 2D models with uniform decreases in potential size the

higher frequencies were when either density or area were the metric, but for geometric regular packing the highest frequency were with the linear metric of the packing. Similarly for the 3D models with uniform decreases in potential size the highest frequency was with the volume metric, but where there was greater difference between potential species sizes, the relationships were with density, linear or area.

Within the packing models with differing decreases in potential size there was no indication of any trend between goodness-of-fit and potential size. It was noted earlier that in simulation of those models that individuals had only reached a proportion of their potential sizes.

The above approach for selecting the best model(s) begs the question of their possible universality when model selection is at least partly determined by the empirical observations at hand. The third approach is to use external criteria for determining the type of models to be considered and the likely metric for abundance in the empirical observations.

As the interest was in the resulting species SAD, the first criteria could be confining model types to those in which individuals are considered for their species identity irrespective of their size.

The second criteria could be matching of models with the type of empirical observations. Matching of empirical density observations with species density packing models would be an example. The matching of other forms of empirical measurements and model type would be more ambiguous. Packing models using the area metric may be appropriate for vegetation measurements of species cover from a ground cover or light intercept perspective. For species bulk or biomass measurements the appropriate packing models could be with either those for area or volume metric.

The first set of empirical observations were divided into density, cover or biomass measurement groups and tested against the corresponding metric packing and other models.

The dismantling models featured in the best six models in all three groups. Two of these were the models of random initial proportion, random selection, and allocation of released domain to the next highest ranked species or other randomly selected species (i_RN, m_RR). Common to those models and as noted earlier, were features of a log-normal distribution (Figure 2). Two of the assembly models also featured – the new arrival model for density and the MacArthur broken-stick model for cover (i_NA, l_BS).

Among the better of the particle packing models was that for uniform size decreases, alternate arrival and growth, and displacement if surrounding were less than rather than less than or equal. It applied to both density and to biomass with the metric for volume (Figure 4 j_Osd, m_Osv).

For cover, two the better models were either 2D for alternate arrival and growth, duration proportional to species potential size and displacement again less than (Figure 2 m_Jsa)(,HH), or 3D with species inserted at their final size and no allowable displacement (m_Csa).

For biomass, the other two of the better fitting models were either similar to the better one with displacement less than or equal and duration proportion to current individuals size and metric volume (Figure 4 i_Msv, l_Nsv), or the 10-species self thinning models with high allowable duration at one size and the metric area (Figure 4 l_Ysa). Differences between the three packing models on the resulting SAD were small. The geometric regular packing models did not feature among the better models.

The present investigations on packing models had been prompted by an allied study following the changes in composition when twenty pasture species had been seeded at randomly selected close fixed points in a small field trial and presence noted and harvested at the scale of individual plants on four occasions over a period of four months (Scott, 2012). That data gave changes in both species density and biomass. The same set of present models was evaluated on that data. With simultaneous consideration of fit to both the density and biomass the 3D self-thinning random particle packing models were best (VWXYZ), with a trend towards geometric regular packing models in the last harvest (S2).

In the present study, though the quadratic fit to individual observations were only among the ‘best-fit’ in about a quarter of the occasions, the principal component plotting field for all the models did separated relatively well in relation to the two coefficients and isopleths for those are given (Figure 4D). The separation was least satisfactory in the left sector of the scattergram where strict log/linear relationships would occur. The coefficient ‘a’ of the quadratic equates with the ‘k’ parameter of the geometric series model when the ‘b’ coefficient is zero and is the starting gradient of the SAD in other situations.

In most of the paper the rank values have been expressed as relative to the most abundant=100. The same results would apply when each were expressed as their proportions of the total community. However, expression in

those terms show the feature, present in both empirical observations and the models, that there is least variation in the contribution of the second and third ranked species, irrespective of the first or later ranked species, with those two generally in the range of 10-20% of the total.

15. Discussion

The investigation and simulation of particle packing models as analogues of ecological community formation was both encouraging and disappointing. In comparison with empirical observations they were at least as good as other existing random assembly or suggested random dismantling models and are offering a possible functional reason for formation of the observed species SADs. They were disappointing in that no single model had superior fit in relation to the different patterns in observed data. That had also been the conclusion from other meta-analysis of other existing models (e.g. Dedney, 2000; Ulrich et al., 2010).

Computer simulation analogue models are good for asking “what if –“ type questions or hypotheses – like “what if the relative abundance of species relates to possible packing configurations of individuals of species of different sizes, different arrival frequencies, growth and mortality rates?”. The hope is that if the results of a simulation studies mimic those of empirical observation then they offer support to the view that those are the ecological processes involved.

The point was made that in most instances, in both analogue modelling and empirical measurements, that the ranking process is retrospective and that that computational process alone will result in a high negative correlation for the SAD's, and may have lulled us into a false impression of the ecological significance of the relationship.

While retaining the negative correlation, there was a large variation in form of the SADs between the different models (Figure 4A). The meta-analysis also showed there was a large variation in empirical data (Figure 4C). Different models fitted different sections of the empirical data. This implies that the question should not be – ‘why should the relationship be generally negative?’, but should be – ‘why of a particular form in a particular situation?’.

The study was proceeding on the possibility that it was the packing of individuals of species of different sizes (in either physical or conceptual space, and either random or regular), determine their relative frequency, total abundance and consequent SADs in ecological communities. The models monitoring the development of random occupation of space by species of equal probability of arrival, but different probability of space occupation, and as analogues offer some possible insights into the process of community formation.

Firstly they develop a community from individuals arriving one-at-a-time rather than collectively as a species, with community statistics only computed at the end.

Secondly individuals arrive in random order with respect to species involved and in that sense are species neutral. The present models used equal probability for arrival of individuals of a species. The same approach could similarly be used for different arrival probabilities.

The third is the changing nature of the relative density of species as a domain becomes successively filled. At the early stages individual of the larger species can find a niche of adequate dimensions. But this option lessens as filling continues, even though retaining equal probability of arrival. At later stages only individuals of smaller sizes can find vacant space.

The effect is that the species size which is first ranked and dominant in terms of total relative abundance (=size*density) changes as filling progresses. At the early stage under uniform probability of size and random arrival the largest sized species is generally the first ranked in total abundance with the successive ranks corresponding to the successive decreasing sizes. But as filling continues there is a shift in the total abundances so that after a high number of successful arrivals the rank order in abundances becomes reversed with the smallest sized species becoming first ranked in terms of its total abundance.

The changes in the gradient of the log SAD during the filling process alter from steep in the initial stages, moderate at intermediate stages, and then returning to steep at later stages. This could be an analogue explanation of the ‘humped backed’ distribution observed in empirical diversity distributions over time.

The fourth aspects relates to dispersion and establishment. The simulations models with constant arrival frequencies were showing that most could find vacant locations early in the simulations but that it dropped to a low level later in the simulations when most sites were already occupied. In another context I have argued that, particularly in biogeography contexts, that we are too quick to equate dispersion (often long-range) with successful establishment (Scott, 1997). The successful establishment of an individual or a species implies both a successful arrival and a

suitable ecological site for its establishment and growth at that point. The probability of each is likely to be low and the combined product very low. It should be possible to obtain empirical evidence of successful dispersion but non-successful establishment (e.g. seed rain).

The fifth aspect was, as expected, that packing was determined by the relative sizes of individuals rather than any taxa species designation, and that that also determined density distributions. Again that is tending to a neutral species view of community formation. Kerkhoff and Enquist (2006) have shown in that many of the features of primary productivity and nutrient levels of can be simulated by allometric scaling related to the frequencies of sizes of individuals in a community.

The paper has not made an assessment of the various models in terms of the maximum entropy considerations.

A more speculative aspect is whether the relative abundance of successive species could correspond to the decreasing possible maximum packing of the largest species as dimensionality of an environment might increases. Peli and Nooteboom (1999) have applied the sphere packing concept to the understanding of generalist and specialist enterprises in a crowded economy. Their concept has interesting analogues for niche separation in ecological communities. They refer to Conway and Sloane's (1988) results showing that as the possible number of space dimensions increase, that the maximum space that can be occupied by the largest (dominant) (hyper)sphere at probable maximum packing density rapidly decreases (maximum possible packing density for largest hypersphere 2D = 91%, 3D = 74%, 4D = 62%, ---- 10D = 10%). This reduction results in the increasing space or abundance for smaller sized spheres. This reduction would be more so in random packing (maximum packing of dominant spheres in 3D of 74% compared to average values of 58-60% in random packing (Gopalakrishnan & Shashidhar, 2006)). There are also estimates of how much the dominant would have to increase in size with changes in dimensionality to maintain its proportion of the total.

The ecological analogue would be of an initial site dominated by a single environmental limiting factor, diverging in space or time into a more multi-factor environment with the specialisation of species into different niches. Note that in the concept that it is not the consideration of the relative size of species per se. related to a physical space, but rather the ecological dimensionality of that space. This is similar to our use of principal component or canonical analysis of ecological observations with an increasing number of factors (dimensions). This effect of dimensional considerations also suggests that fractals could be involved.

Another aspect alluded to in the results is that while maximum packing may relate to boundary conditions of occupation of space, that the functional relationship or effects of species may be with other aspects of the dimensions e.g. collective linear for a species, or collective surface area or volume, or even just the characteristics of individuals themselves.

The present models were initially based on the particle packing of circle areas in 2D or sphere volumes in 3D. The SAD could also be derived if the empirical measurements had been based on individuals, or cumulative linear or area measurements of the same configurations.

There was a changing relationship between species in the particle packing models according to the metric used for abundance. Often the smallest sized species was the first ranked using density and reversed to the largest size species if the volume was used. Consequently there was some intermediate stage when the proportional contribution of species was relatively similar as the models move through the power series of radii size from zero, linear, area to volume. The metric giving the minimum gradient (= equal contribution of species) of the SAD for each of the models was given in the tables.

The implications of the relative fit of different particle packing models is that in considering competition in community formation that perhaps more consideration should be given to the interactions of individuals of different sizes rather than as species per se., though there will be a strong interaction with the potential sizes attainable by different species. The models were also suggesting that SADs were more determined by displacement considerations than by allowable potential lifespan of individuals.

Most of the random particle packing models described in the present study used different 'species' of discrete fixed sizes in equal decreases in potential sizes. By contrast the regular packing models defined both the density and sizes of successive species with the difference in sizes irregular and general greater for the first few ranked species. There is need to look further if there is any pattern relating to the distribution in potential species sizes – perhaps even random. Also studies in the other fields suggest that the same features apply to continuous distributions as to discrete distributions and apply whether they are gradation of sizes in one 'species', or a mixture of different 'species'. Those options were beyond the computing resource I had available. The total packing achieved by all the random packing models was still relatively low relative to theoretical maximum

packing. Mostly that was due to vacant spaces remaining between individuals through random selection of circle or sphere centres, overlapping criteria, and bounds on an individual's size.

In the 2D loose packing model for uni-sized discs (= a single species) inserted at their final size the packing had reached 53.4% though still slowly increasing at the extent the iterations were taken (Figure 1). A similar simulation model for tighter packing had achieved 82% as compared to 78.5% for regular square packing (Visscher & Bolsterli, 1972).

There is the light-hearted definition that the difference between animals and plants is that for animals we can define an individual but not its location, whereas for plant it is the reverse. This is reflected in the different approach to modelling of population dynamics and SADs in plant and animal ecology (e.g. Ulrich et al., 2010). The use of numerical abundance (=density) has dominated in animal ecology and demography and has been transferred into forest ecology. That is not how shrubland, grassland ecologists or agriculturists generally view abundance – hence the relevance of which metric is used for abundance in developing SADs.

The gradient of the SAD of many of the models was relatively shallow implying relatively equal contribution by different species. The particle packing models had shown almost all have some shallow gradient form depending on which metric for abundance is used. There was also large random component in several of the parameters of the better fitting assembly and dismantling models. Both aspects could be carried further to imply that species designation could be neutral and/or dependent on which abundance metric is considered.

While the present study raises caution on the ecological significance of the SAD form as a functional ecological invariant, it does continue to offer a pragmatic method of sampling communities because of the relative ease of assessing the rank order of species. The difficulty is then of ascribing proportional contributions to each of the rank positions. The models described have not suggested proportions that could be universally applied. The Australian dry-weight-rank use constant proportions for the first three rank species in sub-plot samples. In my version of the method there is both the ranking of species and the estimation of the ratio of two of them to give the gradient of an assumed log/linear relationship (Scott, 1989). The present analysis of empirical observations had shown that a quadratic fit to individual samples gave a better general fit. At the field sampling level that would require the estimation for three species – say the ratio of the relative abundance of both the third and sixth species relative to the first – and not extrapolating the proportions outside the number of species considered.

References

- Bell, G. (2000). The distribution of abundance in neutral communities. *American Naturalist*, 155, 606-617. <http://dx.doi.org/10.1086/303345>
- Buckley, H. L., & Freckleton, R. P. (2010). Understanding the role of species dynamics in abundance-occupancy relationships. *Journal of Ecology*, 98, 645. <http://dx.doi.org/10.1111/j.1365-2745.2010.01650.x>
- Chave, J. (2002). Neutral theory and community ecology. *Ecological Letters*, 7, 241-253. <http://dx.doi.org/10.1111/j.1461-0248.2003.00566.x>
- Chave, J, Alons, D., & Etienne, R. S. (2006). Theoretical biology- comparing models of species abundance. *Nature*, 441, E1. <http://dx.doi.org/10.1038/nature04827>
- Conway, J. H., & Sloane, N. J. H. (1988). *Sphere packing, lattices and groups*. A Series of Comprehensive Studies in Mathematics n. 290 Berlin, Springer Verlag. <http://dx.doi.org/10.1007/978-1-4757-2016-7>
- Dewdney, A. K. (2000). A dynamic model of communities and a new species-abundance distribution. *Biological Bulletin*, 198, 152-165. <http://dx.doi.org/10.2307/1542811>
- Díaz, S., Hodgson, J. G., Thompson, K., Cabido, M., Cornelissen, J. H. C., Jalili, A., ... Zak, M. R. (2004). The plant traits that drive ecosystems: evidence from three continents. *Journal of Vegetation Science*, 15, 295-304. [http://dx.doi.org/10.1658/1100-9233\(2004\)015%5B0295:TPTTDE%5D2.0.CO;2](http://dx.doi.org/10.1658/1100-9233(2004)015%5B0295:TPTTDE%5D2.0.CO;2)
- Dodds, P. S., & Weitz, J. S. (2002). Packing-limited growth. *Physical Reviews*, E65, 056108. <http://dx.doi.org/10.1103/PhysRevE.65.056108>
- Enquist, B. J., & Niklas, K. J. (2001). Invariant scaling relations across tree-dominated communities. *Nature*, 410, 655-660. <http://dx.doi.org/10.1038/35070500>
- Gopalakrishnan, K., & Shashidhar, N. (2006). Structural characteristics of three-dimensional random packing of aggregates in wide size distribution. *International Journal of Information Technology*, 3, 201-208.
- He, F. (2010). Maximum entropy, logistic regression, and species abundance. *Oikos*, 119, 578-582. <http://dx.doi.org/10.1111/j.1600-0706.2009.17113.x>

- He, F., & Zillio, T. (2010). Inferring species abundance distribution across spatial scales. *Oikos*, *119*, 71-80. <http://dx.doi.org/10.1111/j.1600-0706.2009.17938.x>
- Holyoak, M., Loreau, M., & Strong, D. (2006). Neutral community ecology. *Ecology*, *87*, 1368-1369. [http://dx.doi.org/10.1890/0012-9658\(2006\)87%5B1368:NCE%5D2.0.CO;2](http://dx.doi.org/10.1890/0012-9658(2006)87%5B1368:NCE%5D2.0.CO;2)
- Hubbell, S. P. (1979). Tree dispersion, abundance and diversity in a dry tropical forest. *Science*, *203*, 1299-1309. <http://dx.doi.org/10.1126/science.203.4387.1299>
- Hubbell, S. P. (2001). *A Unified Neutral Theory of Biodiversity and Biogeography*. NJ: Princeton University Press.
- Kerkhoff, A. J., & Enquist, B. J. (2006). Ecosystem allometry: the scaling of nutrient stocks and primary productivity across plant communities. *Ecological Letters*, *9*, 419-427. <http://dx.doi.org/10.1111/j.1461-0248.2006.00888.x>
- Loehle, C. (2006). Species abundance distributions result from body size-energetic relationships. *Ecology*, *87*, 2221-2226. [http://dx.doi.org/10.1890/0012-9658\(2006\)87%5B2221:SADRFB%5D2.0.CO;2](http://dx.doi.org/10.1890/0012-9658(2006)87%5B2221:SADRFB%5D2.0.CO;2)
- McGill, B. J., Enquist, B. J., Weiher, E., & Westoby, M. (2006). Rebuilding community ecology from functional traits. *Trends in Ecology & Evolution*, *21*, 178-185. <http://dx.doi.org/10.1016/j.tree.2006.02.002>
- Morlon, H., White, E. P., Etienne, R. S., Green, J. L., Ostling, A., Alonso, D., ... Zillio, T. (2009). Taking species abundance distributions beyond individuals. *Ecological Letters*, *12*, 488-501. <http://dx.doi.org/10.1111/j.1461-0248.2009.01318.x>
- McGill, B. J., Maurer, B. A., & Weiser, M. D. (2006). Empirical evaluation of neutral theory. *Ecology*, *87*, 1411-1423. [http://dx.doi.org/10.1890/0012-9658\(2006\)87%5B1411:EEONT%5D2.0.CO;2](http://dx.doi.org/10.1890/0012-9658(2006)87%5B1411:EEONT%5D2.0.CO;2)
- Peli, G., & Nooteboom, B. (1999). Market partitioning and the geometry of the resource space. *American Journal of Sociology*, *104*, 1132-1153. <http://dx.doi.org/10.1086/210138>
- Pettijohn, F. J. (1975). *Sedimentary rocks*. Harper & Bros., New York.
- Preston, F. W. (1948). The commonness and rarity of species. *Ecology*, *29*, 254-283. <http://dx.doi.org/10.2307/1930989>
- Roxburgh, S. H., & Mokany, K. (2010). On testing predictions of relative abundance from maximum entropy optimisation. *Oikos*, *119*, 583-590. <http://dx.doi.org/10.1111/j.1600-0706.2009.17772.x>
- Scott, D. (1965). A height frequency method for sampling tussock and shrub vegetation. *New Zealand Journal of Botany*, *3*, 253-260. <http://dx.doi.org/10.1080/0028825X.1965.10429019>
- Scott, D. (1989). Description of vegetation interactions using visual ranking of species. *New Zealand Journal of Ecology*, *12*, 77-88.
- Scott, D. (1977). Plant ecology above timberline on Mt Ruapehu I. Site factors and plant frequency. *New Zealand Journal of Botany*, *15*, 255-294. <http://dx.doi.org/10.1080/0028825X.1977.10432546>
- Scott, D. (1997). Ecological considerations in plant invasion, with New Zealand examples. In E. Yano, K. Matsuo, M. Shiyomi & D. A. Andow (Eds.). *Biological invasion of ecosystems by pests and beneficial organisms*. pp.109-121.
- Scott, D. (2006). Constancy in pasture composition? Empirical measurements and mathematical models. *New Zealand Journal of Agricultural Research*, *49*, 183-190. <http://dx.doi.org/10.1080/00288233.2006.9513708>
- Scott, D. (2012). Vegetation productivity/stability and other possible ecological invariant relationships demonstrated in a micro-plot multi-species pasture sward. *Open Ecology Journal*.
- Scott, D., & Billings, W. D. (1963). Effect of environmental factors on standing crop and productivity of an alpine tundra. *Ecological Monographs*, *34*, 243-270. <http://dx.doi.org/10.2307/1948502>
- Scott, D., Dick, R., & Hunter, G. (1988). Changes in the tussock grasslands in the Waimakariri River basin, Canterbury, New Zealand from 1946 to 1981. *New Zealand Journal of Botany*, *26*, 197-122. <http://dx.doi.org/10.1080/0028825X.1988.10410113>
- Shipley, B. (2009). *From plant traits to vegetation structure: Chance and Selection in the Assembly of Ecological Communities*. UK: Cambridge University Press, Cambridge. <http://dx.doi.org/10.1017/CBO9780511806971>
- Soddy, S. (1936). The kiss precise. *Nature*, *137*, 1021. <http://dx.doi.org/10.1038/1371021a0>
- Sohn, H. Y., & Moreland, C. (1968). The effect of particle size distribution on packing density. *Canadian Journal of Chemical Engineering*, *46*, 162-167. <http://dx.doi.org/10.1002/cjce.5450460305>

- Stoeven, P., & Stroeven, M. (1999). Assessment of packing characteristics by computer simulation. *Cement and Concrete Research*, 29, 1201-1206. [http://dx.doi.org/10.1016/S0008-8846\(99\)00020-4](http://dx.doi.org/10.1016/S0008-8846(99)00020-4)
- Tokeshi, M. (1990). Niche apportionment or random assortment: species abundance patterns revisited. *Journal of Animal Ecology*, 59, 1129-1146. <http://dx.doi.org/10.2307/5036>
- Ulrich, W., Ollick, M., & Ugland, K. I. (2010). A meta-analysis of species-abundance distributions. *Oikos*, 119, 1149-1155. <http://dx.doi.org/10.1111/j.1600-0706.2009.18236.x>
- Visscher, W. M., & Bolsterli, M. (1972). Random packing of equal and unequal spheres in two and three dimensions. *Nature*, 239, 504-507. <http://dx.doi.org/10.1038/239504a0>
- Wardle, P. (1991). *Vegetation of New Zealand* (p. 672). Cambridge: Cambridge University Press.
- Wilson, J. B. (1999). Assembly rules in plant communities. In E. Weiher & P. Keddy (Eds.), *Ecological assembly rules – perspectives, advances, and retreats* (p. 418). Cambridge, Cambridge University Press. <http://dx.doi.org/10.1017/CBO9780511542237.006>
- Williams, E. (1978). Botanical composition of the Park Grass plots at Rothamsted 1856-1976. *Rothamsted Experimental Station*, 61.
- Whittaker, R. H. (1972). Evaluation and measurement of species diversity. *Taxon*, 21, 213-251. <http://dx.doi.org/10.2307/1218190>

Copyrights

Copyright for this article is retained by the author(s), with first publication rights granted to the journal.

This is an open-access article distributed under the terms and conditions of the Creative Commons Attribution license (<http://creativecommons.org/licenses/by/3.0/>).