



Assessing evidence for random assembly of marine benthic communities from regional species pools

P. J. Somerfield^{1,*}, C. Arvanitidis, S. Faulwetter, G. Chatzigeorgiou, A. Vasileiadou, J. M. Amouroux, N. Anisimova, S. J. Cochrane, J. Craeymeersch, S. Dahle, S. Denisenko, K. Dounas, G. Duineveld, A. Grémare, C. H. R. Heip, M. Herrmann, I. Karakassis, M. Kędra, M. A. Kendall, P. Kingston, L. Kotwicki, C. Labrune, J. Laudien, H. Nevrova, A. Nicolaidou, A. Occhipinti-Ambrogi, R. Palerud, A. Petrov, E. Rachor, N. Revkov, H. Rumohr, R. Sardá, U. Janas, E. Vanden Berghe, M. Włodarska-Kowalczyk

¹Plymouth Marine Laboratory, Prospect Place, West Hoe, Plymouth PL1 3DH, UK

ABSTRACT: Local species diversity may be determined by processes operating locally, such as disturbance, predation and competition, or by regional processes, such as environmental structuring or history. Classical theory focusing on competition predicts that the species combining to form communities will be less similar to each other than they would be if they were assembled at random from a regional species pool. Theory focusing on environmental structuring predicts that species will be more similar to each other than expected by chance. A randomisation test that determines the extent to which local species lists represent random selections from a regional list, based on the average relatedness between species, was applied to data held in the MacroBen database. Little or no evidence was found for species lists of whole faunas at any scale being random subsets of species lists at larger scales. Species tend to be more closely related to each other than would be expected if they were assembled at random. Thus marine soft-sediment macrofauna are not locally assembled at random from regional species pools and it is likely that regional processes determine the assembly of communities. Focusing on the most abundant class within the macrofauna, a different pattern emerges, in that there is a much stronger tendency for local polychaete composition to be a random subset from regional pools at all scales. Thus it is not possible to determine whether local polychaete diversity is independent of both local and regional processes, or determined by a combination of both acting antagonistically.

KEY WORDS: Benthos · Soft sediment · Community assembly · Local–regional relationships · Species pools · Taxonomic distinctness

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INTRODUCTION

The idea that species occurring in a particular place at a particular time are not simply a random collection is not new (Raunkjær 1934, Williams 1947) and there have been a number of attempts to model the way in which actual communities come to be (Diamond 1975, Tofts & Silvertown 2000). In essence, studies focus on the relationship between local (however defined) species composition and species pools reflecting species which could occur in the local assemblage (regional pools). Assembly is considered to be a fundamental

process underpinning the construction and evolution of biological systems (Drake 1990), and there are 2 views of how non-randomness in species composition arises and how it relates to the set of potential colonists. Many ecological studies focus on interactions between organisms, generally concluding that competition is of primary importance in determining species composition and that competition is greatest between those species that are most similar (e.g. Johansson & Keddy 1991, Wilson & Watkins 1994, Wilson & Gitay 1995), so communities are most stable when coexisting species are dissimilar and traits are overdispersed with

*Email: pjs0@pml.ac.uk

respect to an appropriate null model. An alternative viewpoint (e.g. Schimper 1903, Tofts & Silvertown 2000) is that, given a set of environmental conditions, only species possessing certain subsets of attributes will be able to establish themselves in a community, leading to an assemblage in which traits are under-dispersed with respect to a null model.

Issues concerning assembly rules, and the appropriateness of null models, have been the subject of vigorous debate amongst ecologists for decades (Weiher & Keddy 1999). Although it is possible to construct hypotheses concerning the randomness or otherwise of local community assembly from regional species pools, in practice it is far from straightforward to construct sensible statistical tests to examine such hypotheses. Several studies have correlated local species richness with regional species richness across different communities (e.g. Cornell 1985a,b, Ricklefs 1987, Caswell & Cohen 1993), interpreting non-linearities in the relationship between local and regional species numbers as evidence of 'saturation' (Srivastava 1999, Loreau 2000). Another approach has been to model assembly explicitly using, for example, patch-occupancy models (Caswell & Cohen 1991, 1993, Hugueny et al. 2007). A problem with such approaches is that they tend to exclude details of the relationships between species, or at best to examine them rather superficially, focusing on numerical distributions rather than taxonomic or ecological similarities or differences between organisms.

One approach to investigating community assembly has been to examine variation in taxonomic ratios, such as the ratio between numbers of species and numbers of genera (Elton 1946, Williams 1947). This implies that the relatedness of species in assemblages may provide useful insights into community assembly. Measures based on the taxonomic (Warwick & Clarke 2001) or functional (Sommerfield et al. 2008) relatedness of species provide an alternative view of biodiversity to that based on numbers alone. Clarke & Warwick (1998) demonstrated that average taxonomic distinctness (Δ^+), the mean path-length between species in a list through a taxonomic tree, has useful statistical properties. If all species in a regional list are equally likely to appear in a local assemblage, the measure is sample-size independent, and Clarke & Warwick (1998) present a randomisation test that specifically addresses the question of whether 1 species list represents a random subset of species from another. Such a test provides the opportunity to address relationships between local and regional species lists explicitly. In addition to the general ecological interest in assembly rules, there is also a practical aspect to understanding relationships between local and regional species pools. Indices of relatedness, and their associated randomisation tests,

have been proposed as measures of stress in communities (Warwick & Clarke 1995, 1998, 2001); species in stressed assemblages tend to be more closely related to each other than expected. For indices of relatedness and their associated randomisation tests to be generally applicable, we need to know what the appropriate regional pool may be against which to test a local species list.

In the present study we apply Clarke & Warwick's (1998) test to species occurrences in a large number of samples of macrobenthic infauna from across the European continental shelf to address 2 main issues: (1) Is there evidence that species within assemblages are assembled at random from regional species pools at larger spatial scales? (2) If so, are there appropriate scales for defining local and regional species pools? It is arguable whether studies of relatedness within assemblages should be restricted to taxonomically coherent groups (Clarke & Warwick 2001, Ellingsen et al. 2005). To assess this, analyses were conducted using occurrence data for all macro-infauna, and then repeated using only occurrence data for the most abundant class, the polychaetes.

DATA AND METHODS

Data. The MacroBen database contains nearly 0.5 million distribution records of 7203 taxa at 22 897 stations; a full description is given in Vanden Berghe et al. (2009, this Theme Section). A major effort was made to harmonise the taxonomy across the different datasets within the database: all names were matched, both for spelling and synonymy, with the European Register of Marine Species (ERMS; www.marbef.org/data/erms.php). Raw data were retained whenever possible to allow maximum flexibility during analyses. Most data providers also furnished geographical and physical data. To work with the most inclusive, yet most comparable, dataset possible, we performed initial filtering on the database. Datasets for which subtidal soft-sediment samples were collected with 0.1 m² grabs, sieved on 0.5 or 1 mm meshes and abundances recorded to the species level were selected. For taxonomic consistency, only datasets collected after 1980 were included, and to avoid confounding, samples known to be affected by natural or anthropogenic stressors were excluded. Where possible, datasets with repeated observations (e.g. multiple grabs from each station) were chosen to allow tests at the lower levels (e.g. individual grabs against stations). The main focus of the present study was adult macro-infauna, so taxa identified as juveniles or colonial animals (e.g. Bryozoa, Hydrozoa, Porifera) were excluded, as were samples containing <5 species, as relatedness measures

based on very few species are too variable to be of use. The resulting database, on which the present study is based, contained information on the distributions of 2477 species, comprising 63 281 occurrences distributed among 1238 samples derived from 31 original datasets from continental shelf locations distributed from the Arctic to the Black Sea (Table 1).

Local and regional species lists. There is no universally agreed or sensible definition of what constitutes a location or a region for the purposes of comparing local and regional diversity, or determining how local diversity reflects regional patterns. All that matters for the definition is that the regional list is larger than the local list. We took a hierarchical approach to examining local/regional relationships. Within the database we defined a number of hierarchical groupings of samples, reflecting how an investigator might choose to

define species lists for the purposes of conducting tests: individual samples (grabs) within stations, stations within surveys, surveys within regions and regions within the complete database. Tests were conducted for all pairs of levels, except samples against the regional lists and the European list (being the complete list of species from all of the samples in the database), as the computational demands of such tests would have been very large. Thus species lists from individual grabs were tested against the combined species list from the station at which they were collected. Lists from each sample and combined lists from each station were tested against the combined list from the survey at which they were collected. Lists from each station and each survey were tested against combined lists from areas within regions, defined using a range of schemes, within which they were collected.

Lists from stations, surveys, and regions (areas within regional schemes) were tested against the European list, the combined list from all soft-sediment samples in the database.

Several regional schemes were used to divide European waters into areas, reflecting different ways in which an investigator might attempt to construct 'regional' lists for the purposes of tests of relatedness. These were: the scheme proposed by Fredj (1974); areas defined by the International Council for the Exploration of the Seas (ICES; www.ices.dk/aboutus/icesareas.asp); regional seas proposed by the International Hydrographic Organization (IHO 1953); large marine ecosystems (LMEs; www.lme.noaa.gov/Portal/) reviewed by Sherman (1994); regions defined by the Oslo-Paris Commission (OSPAR) for the Quality Status Report process; and biogeochemical provinces described by Longhurst (1998). A more detailed description of these classifications (and their relative merits) can be found in Arvanitidis et al. (2009, this Theme Section).

Statistical analysis. The complete set of analyses was conducted using all macrofaunal species in samples (with the exception of those excluded using the criteria outlined in 'Data'), and again using only species within the most abundant class, namely the polychaetes.

Average taxonomic distinctness (Δ^+), a measure of the average degree to which species in an assemblage are related to each other, is defined as:

Table 1. Summary of sources of data used. For details see Vanden Berghe et al. (2009, this Theme Section). Shown are numbers of samples and stations used following data filtering, and proportion of the total provided by those surveys contributing $\geq 1\%$. Parentheses: fewer samples or stations used for analyses of polychaete data following data filtering

Survey	Code	Samples		Stations	
		No.	%	No.	%
Arctic Ocean and Barents Sea	ar			22	2
Franz Josef Land	o8	45	2	9	1
Kongsfjord, Spitzbergen	ko			6	
Hornsund, Spitzbergen	hs			34	3
Northern Barents Sea	o2	44	2	10	1
Pechora Sea	o7	71 (66)	3	15 (14)	1
Finmark	o6	275	11	53	4
Norwegian and Barents Seas	o4	1146 (1091)	45	183 (129)	15
North and Norwegian Seas	o3	269 (262)	10	30 (26)	2
Bay of Puck	pu			29	2
Gulf of Gdansk	gd			13	1
Kiel Bay N3	n3	321	12	1	
Kiel Bay intercalibration	70	70	3	1	
North Sea benthos survey	ns			231	19
BIOMÔR ^a	o5			51	4
Blanes Bay	bl			2	
Redit	gr			92	7
LBMRev	lm			28	2
Cesenatico	oc			1	
Cretan shelf	ka			199	16
Crete (Mop)	do			56	5
Mytilini	M2	71 (70)	3	9	1
Saronikos	M3	76 (74)	3	6 (5)	
Kalamitsi	M6			22	2
Kerkyra	M7			12	1
Kyklades	M8	55	2	14	1
Gialova	M0	134 (116)	5	7 (6)	1
Megfeod	M1			24	2
Strel Bay	M4			18	1
Jalta	M5			26	2
Laspi Bay	M9			33	3

^aData from Mackie et al. (1995)

$$\Delta^+ = [\sum \sum_{i < j} \omega_{ij}] / [s(s-1)/2] \quad (1)$$

where s is the number of species present, the double summation is over $\{i = 1, \dots, s; j = 1, \dots, s, \text{ such that } i < j\}$, and ω_{ij} is the 'distinctness weight' given to the path length linking species i and j in a hierarchical classification (Clarke & Warwick 1998). As advocated by Clarke & Warwick (1998), values of Δ^+ were based on equal step-lengths between taxonomic levels. For macrofauna, the taxonomic levels used in the present study were species, genus, family, order, class and phylum, according to the classification contained within the ERMS. Thus the step-length between adjacent taxonomic levels was 16.67, e.g. for different species in the same genus $\omega = 16.67$, for species in different genera, but the same family $\omega = 33.33$, for species in different families, but the same order $\omega = 50$, etc., and $\omega = 100$ for species connected at the highest (taxonomically coarsest) level. For polychaetes the levels were species, genus, order and class, and step-lengths ($\omega = 25$) were adjusted accordingly.

Values of Δ^+ calculated for 'local' species lists were compared with the expected range of values from 'regional' lists using the routine TAXDTEST in the PRIMER software (Clarke & Gorley 2006). Subsets of m species, where m is the number of species in the local list, were drawn at random from the regional list and Δ^+ calculated. The value of Δ^+ was calculated from the local species list was compared with the distribution of Δ^+ values from a large number (1000 in the present study) of random draws from the regional list. If the observed Δ^+ fell outside the central 95% of the simulated Δ^+ values, it was considered to have departed significantly from expectation: a 2-sided test was appropriate since departure may theoretically be in the direction of enhanced as well as reduced distinctness. The result of each of the >1000 tests was treated as an independent observation for the purpose of calculating confidence intervals about the mean number of tests falling within 95% probability intervals for tests at each level. It could be argued that a series of tests for samples from a particular dataset against a single species list are not strictly independent, but we took the view that any apparent decrease in variability between observations introduced by such a lack of independence would be counterbalanced by the range of surveys included at each level.

RESULTS

Fig. 1 is a highly condensed summary of results from tests at all spatial levels. If species are behaving as if assembled at random from the regional species pool, then on average 95% of tests should fall within the

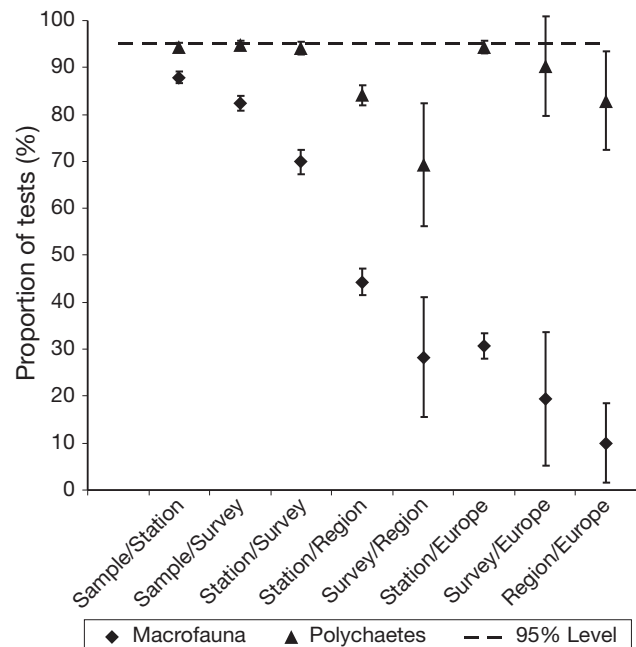


Fig. 1. Summary of randomisation tests at all spatial levels. Values on the y-axis are the average percentage of species lists ($\pm 95\%$ CI) for which average taxonomic distinctness (Δ^+), calculated from combined lists at the level of the first category (= 'local' lists) on the x-axis label, falls within the 95% probability levels of Δ^+ calculated from the appropriate combined lists at the level of the second category (= 'regional' lists). Values were averaged across all datasets for each pair of levels. Values were re-averaged across regional schemes for comparisons involving regions. All tests were repeated for macrofauna and for polychaetes. The 95% line indicates a level at which it might be reasonable to assume that the hypothesis of assembly at random cannot be rejected

95% probability limits for those tests. Thus the confidence intervals for the mean number of tests falling within those 95% limits should also encompass the 95% line in Fig. 1. For macrofauna the pattern is very clear. For no pair of scales (local and regional) does the local species list represent a random subset of the regional list, since in all cases the percentage of local samples falling within 95% probability limits for Δ^+ derived from the regional list is <95%. Although not illustrated here, the general tendency is for species to be more closely related to each other (samples falling below the lower 95% limit). As the areas from which both local and regional species lists are derived increase, so the tendency for Δ^+ values to fall below expectation (i.e. rejecting the hypothesis of random assembly) also increases (Fig. 1). Similarly, as the mismatch in spatial scale between localities and regions increases, the hypothesis of assembly at random from the regional pool appears less likely to be true.

Confining the analyses to tests of random assembly within the polychaetes (Fig. 1) produces a very differ-

ent pattern. While a rigid adherence to the idea that a value of 95% must be achieved in order to reject the null hypothesis (assembly is not random) would allow the conclusion that there is no evidence that the null hypothesis is falsified, it is very clear that values in many cases approach this value and the confidence intervals about the mean include the 95% value. Thus a hypothesis of random assembly of local communities from regional pools is plausible at the scales of samples versus stations and surveys, stations versus surveys, or even stations and surveys versus the whole European fauna collected in all of the surveys (Fig. 1). All values are very much higher than for macrofauna and the clear relationships between area, differences in scale and the likelihood of the null hypothesis being false, which were evident for the macrofauna, are less apparent for analyses based on polychaetes alone. Of all the different groupings of samples it is those associated with the regional schemes that show evidence for non-random assembly.

DISCUSSION

The recognition that the numbers of species in local communities are not governed solely by processes operating at local scales and that regional biogeographical processes are also important (Ricklefs 1987, Ricklefs & Schluter 1993) represented a paradigm shift in community ecology (Loreau 2000). Most studies examining relationships between local and regional species numbers (e.g. Cornell & Lawton 1992, Srivastava 1999) have found evidence for local richness increasing with regional richness, as if local communities are obtained by proportional sampling from the regional pool (Loreau 2000). Prior to this, questions concerning the degree to which species within communities are assembled at random, or if not, then how, and how one can tell, had been the subject of vigorous debate (Connor & Simberloff 1979, Diamond & Gilpin 1982, Gilpin & Diamond 1982) which is by no means resolved to this day (Weiher & Keddy 1999). More recent developments, such as the unified neutral theory of biodiversity and biogeography (Hubbell 2001), have led to a reexamination and reevaluation of many of the issues involved (Bell et al. 2006, Holyoak & Loreau 2006, Hubbell 2006, McGill et al. 2006), still with conflicting results and interpretations.

Coupled with this, and relevant to the present work, are developments in the incorporation of phylogenetic information into community ecology (e.g. Webb et al. 2002, Helmus et al. 2007), often using measures that are simple mathematical transformations of Clarke & Warwick's taxonomic diversity and taxonomic distinctness (Warwick & Clarke 1995, Clarke & Warwick

1998), which in turn are closely related to Rao's quadratic entropy (Rao 1982). Species which are closely related might have similar tolerances to environmental stressors, and would thus be expected to occur within the same communities (Webb 2000) or, conversely, closely related species may have similar resource requirements, leading to inter-specific competition and exclusion from communities (Elton 1946). The emphasis here is on relatedness, which may be reflected in taxonomic similarity, rather than on traits, the assumption being that closely related species will tend to share many traits. While this distinction is important, the resulting hypotheses, that inter-specific interactions will tend to decrease relatedness while environmental or evolutionary factors will tend to lead to communities which are more closely related, are exactly analogous to those outlined in our 'Introduction'.

Against a background of shifting evidence and opinion, alternative methods, and continuing debate about the extent to which local communities are assembled at random from regional species pools, a fundamental issue has to be remembered. 'Local' and 'regional' are relative terms. Loreau (2000) showed that the form of local-regional richness curves is determined by the way total diversity is partitioned between its α and β components, which itself is a matter of scale. Although a few studies exist which have combined 'phylogenetic' relatedness approaches with scale issues (e.g. Kembel & Hubbell 2006, Swenson et al. 2006), none has approached this study in terms of variation in spatial scales.

We show that species within marine macrobenthic communities tend to be more closely related to each other than would be expected if species behave as though assembled at random from regional species pools. This non-randomness increases as the difference in scale between what is considered 'local' and the scale at which the regional pool is defined increases. This may be taken as evidence that at the scales of observation, environmental and evolutionary factors are important determinants of community composition, and inter-specific interactions are not. In marine benthic systems this makes sense. Species in marine systems have evolved to exploit regularities in the physical dynamics of the environment as part of their reproductive processes, and often use diffusive dispersal to counteract the longer-term consequences of variability in the physical environment (Steele 1991). Thus marine systems are relatively dynamic and open, compared to terrestrial systems, and species, even those which are rarely captured, tend to be widely distributed. Conditions where one species may outcompete and exclude closely related species in a marine benthic community at anything other than short time scales and small spatial scales are difficult to

imagine, and community structure can be expected to vary with environmental conditions and to be determined by processes operating over large scales of space and time. A similar conclusion was drawn by Bellwood & Hughes (2001), in a study of fish and coral communities in the Indian and Pacific Oceans.

The pattern within analyses confined to the polychaetes suggests that random assembly is a plausible hypothesis within surveys for this group, and that for groups of samples (stations), polychaete species are a random subset from the European list. Following the reasoning outlined above, it would appear that heterogeneity in environmental conditions and history are less important for polychaete assemblages, and that we cannot distinguish between their effects and the effects of inter-specific interactions. In other words, it is not possible to determine whether local polychaete diversity is independent of both local and regional processes, or determined by a combination of both acting antagonistically. Why, then, do we observe a different pattern when confining our analyses to the polychaetes? It may be something to do with the ecology of polychaetes or their taxonomy. Typical polychaete assemblages are taxonomically and trophically diverse (Fauchald & Jumars 1979, Olsgard & Somerfield 2000). The taxon has received a recent phylogenetic review (Rouse & Pleijel 2001) and, as they are a key component of macrofaunal assemblages, taxonomic expertise is widespread in Europe — factors which may imply a greater homogeneity in approaches among the different datasets combined in our analysis.

On the other hand, it may tell us something about the analytical method. Potential problems with the use of a taxonomic, as opposed to a phylogenetic, classification are discussed by Ellingsen et al. (2005). Leaving that aside, it is to be expected that relatedness measures are heavily influenced by the largest differences between species, namely the distances between species in different taxa at the higher levels in the classification. Although Clarke & Warwick (1999) and Rogers et al. (1999) showed strong insensitivity of Δ^+ to major variations in the branch step-lengths between taxonomic ranks, it is likely that analyses of assemblages with a great deal of structure at higher taxonomic levels will reflect heterogeneity in the balance of species within those higher taxonomic levels. Clarke & Warwick (1999) pointed out that measures such as Δ^+ are not constrained to hierarchies with fixed points of genus, family, order, etc., but carry over naturally and forcefully to continuous phylogenies in which the branch lengths are fully determined, for example by genetic distances (e.g. Nei 1996), so this is not an artifact introduced by the use of a taxonomic classification.

The fact that we observed different relationships between scale and randomness when looking at as-

semblages of mixed phyla as compared to assemblages of polychaetes (which do, after all, contribute a large proportion of species in macrofaunal assemblages) suggests that a useful way forward might be to examine in more detail the way in which species are distributed among higher taxonomic levels, and contribute to measures of relatedness in mixed assemblages. There is a lot of evidence for structural redundancy in marine macrobenthic assemblages, and it is likely that closely related species may be interchangeable in communities (Warwick 1993, Olsgard et al. 1997, 1998), whereas large-scale heterogeneity may influence the distribution of phyla, and species within phyla, in ways that differ. The vast majority of studies considering community assembly and species distributions have focused on species (or populations) as the units of interest. It is possible that analyses focusing on the presence of groups of species, taxonomically or functionally related, may provide insights into the processes structuring communities.

In the meantime, what recommendations can be made for those wishing to examine the idea that assemblages under stress consist of subsets of species which are more closely related to one another than would be expected under a null expectation that all species are equally likely to occur? What are the appropriate scales at which to define 'local' and 'regional' species lists, in order that such tests may be valid? It would appear from the results of the present study that such tests should be based on taxonomically coherent subsets of species. It is worth noting that much of the development work on the testing structure (e.g. Clarke & Warwick 1998) was based on nematode assemblages. Certainly for the polychaetes it appears that, as long as one avoids lists based on the various regional schemes, any combination of 'local' and 'regional' lists may be appropriate. For tests based on whole macrofaunal assemblages, it would appear that a null hypothesis of random assembly with equal probabilities of occurrence is not generally appropriate.

Finally, it must be remembered that the null hypothesis examined here, that species in local assemblages are random subsets of the species in the appropriate regional pool, implies that all species in the regional pool have an equal probability of appearing in any subset. There are a range of other, perhaps more sensible, alternative hypotheses which should be examined (Gotelli 2000, Helmus et al. 2007). For example, most species in assemblages are rare (Gray et al. 2005), and a few are abundant and widely distributed. The simulation of random draws from the regional pool can be constrained to match the probabilities of occurrence of each species, defined by their frequency of occurrence in a large number of samples (Somerfield et al. 2008). Thus certain species will be picked more often

in the random subsets, because they are observed to be present more often in real samples. The hypothesis, therefore, is that species in assemblages are random subsets of a regional pool but their probability of occurrence is determined by processes affecting species abundance distributions, operating independently. This would also fit neatly with the idea that most species patterns observed in nature may be derived from a simple model in which distributions are determined by abundances of species at the largest measured scale (Harte et al. 2005).

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