NOTE

Spatial uniformity of biodiversity is inevitable if the available species are distributed independently of each other

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ABSTRACT: For all general types of frequency of species occurrence curve, the proportion of the total species in unit samples is significantly uniform if the component species are distributed independently of each other, and the precise constant number of species obtained then depends on the shape of the curve. In respect of the recently demonstrated instances of spatial uniformity of macrofaunal species density in intertidal seagrass and in adjacent unvegetated sediment, the observed proportions of samples containing different total numbers of species do not differ from those expected by chance from the observed overall occurrence frequency distributions. The spatial uniformity of species density observed is therefore no more than an inevitable reflection of the frequency of occurrence distributions of the species concerned under conditions of random assemblage composition, and requires no further biological explanation. What produces the similar frequency of species occurrence patterns in seagrass habitats, however, yielding similar numbers of species per unit area from the cool-temperates to the subtropics, remains to be elucidated.

KEY WORDS: Biodiversity · Macrobenthos · Sandflat · Seagrass · Spatial constancy · Spatial occurrence · Spatial uniformity

INTRODUCTION

It has recently been demonstrated, both in intertidal seagrass beds and in adjacent areas of unvegetated sediment, that the biodiversity of benthic macrofauna — assessed as species density, i.e. number of species per unit area (Gotelli & Colwell 2001), down to unit areas of 0.0275 m^2 — shows statistically significant spatial uniformity across distances of up to 6.5 km, notwithstanding marked patchiness of the individual component species populations and consequent non-uniformity of overall assemblage composition (Barnes 2013, 2014). This state occurred in high abundance but low diversity habitats on cool-temperate Scolt Head Island in the North Sea (UK) through to low abundance but high diversity systems in subtropical North Stradbroke Island in Moreton Bay, Queensland, Australia. Within the seagrass, for example, the percentage of the total species pool present per 0.0275 m^2 varied widely from some 48% on Scolt Head to 16% on North Stradbroke, but the actual number of species per unit sample was statistically uniform at each site, with 14.3 ± 0.76 species (mean ± SE) at the cool-temperate site, 20.7 ± 0.40 in warm-temperate Knysna, South Africa, and 22.7 ± 0.65 in Queensland.

The occurrence of temporal uniformity of species density, however, is much more widely suggested (e.g. Pandolfi 1996, Clark & McLachlan 2003), and in this regard it has been argued (Brown et al. 2001, Goheen et al. 2005) that one of the necessary conditions is resource limitation and the operation of deter-

ministic 'assembly rules' of the type proposed by Diamond (1975), Gotelli & McCabe (2002), Weiher et al. (2011) and others. There is a number of reasons why it is most unlikely that this condition can be met by intertidal soft-sediment habitats. (1) All habitats of this type in which spatial uniformity of species richness or diversity has been demonstrated are likely to be held below carrying capacity as a result of predation (Reise 1985, Valentine & Duffy 2006, Lewis & Anderson 2012); (2) probably as a result, the macrofaunal species associations at these sites were all randomly assembled (Barnes & Ellwood 2011), as appears to be the case in many plant and other communities (Hubbell 1997, Götzenberger et al. 2012). Barnes (2014) suggested that besides being below carrying capacity, all the sites concerned also showed a further feature: very similar rank-order frequency of species occurrence distributions, both in percentage frequency form and when expressed as relative proportions of overall species-occurrence totals. Barnes (2014) thought it likely that the phenomena of local uniformity of species density, comparable numbers of species per unit area across disparate systems, random assemblage composition, and similar frequency of occurrence distributions were in some manner related, but was unable to suggest the nature of the relationship.

It is the purpose of this note to demonstrate by further analysis of the data in Barnes (2013, 2014) that spatial uniformity of species density is a consequence of the random nature of the distribution of the component species, whilst the precise values of species density are dependent on the form of the frequency of occurrence curves.
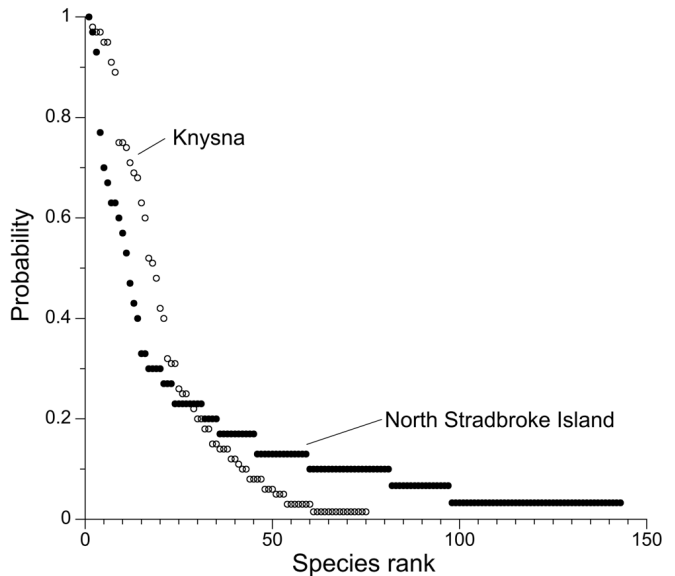

Fig. 1. Probability of occurrence of macrobenthic species in 0.0275 m² samples of intertidal seagrass beds: *Zosterella capensis* in Knysna estuarine bay, South Africa (65 samples; 4600 individuals of 75 species), and *Z. capricorni* on North Stradbroke Island, Moreton Bay, Queensland, Australia (30 samples; 2000 individuals of 143 species)

METHODS

Data on the frequency of occurrence of each species can be presented as the probabilities of each species occurring in unit sample (Fig. 1). For a given number of species per sample, the expected probability of occurrence P_S is then determined as the probability in 10 000 iterative pseudo-samples. The species density of each pseudo-sample is calculated as the sum of the occurrences of each taxon recorded for that locality. The presence/absence of a taxon within a pseudo-sample is determined using the observed probability of occurrence of that taxon P_T and a random number generator such that for any given taxon and any given pseudo-sample, the taxon is deemed present if the observed probability of occurrence (ranging from 1 to 1/n, for n samples) is greater than

the random number (between 0 and 1 generated with 3 significant figures) and deemed absent if the probability of occurrence is less than the random number. This procedure was conducted in Microsoft Excel®. Thus the expected distribution is based on the assumption that species are distributed independently of each other. Whether such observed and expected distribution functions differ significantly can be determined by the Kolmogorov-Smirnov test.

RESULTS AND DISCUSSION

In the 5 habitats that displayed uniform spatial species density in Barnes (2013, 2014), the observed and expected distribution of species per sample under conditions of random assortment were not significantly different (Kolmogorov-Smirnov, p > 0.3) (Fig. 2). Hence in no case does the observed pattern differ from that expected from the frequency of occurrence curves (see Fig. 5 in Barnes 2014) in the absence of assemblage-structuring influences. Assigning probabilities and a reasonable total number of species (e.g. 100) to all frequency of occurrence curves in Jenkins (2011, his Fig. 1) indicates that all such distributions can be expected to yield equally uniform numbers of species per sample if the species are randomly assorted (Standardised
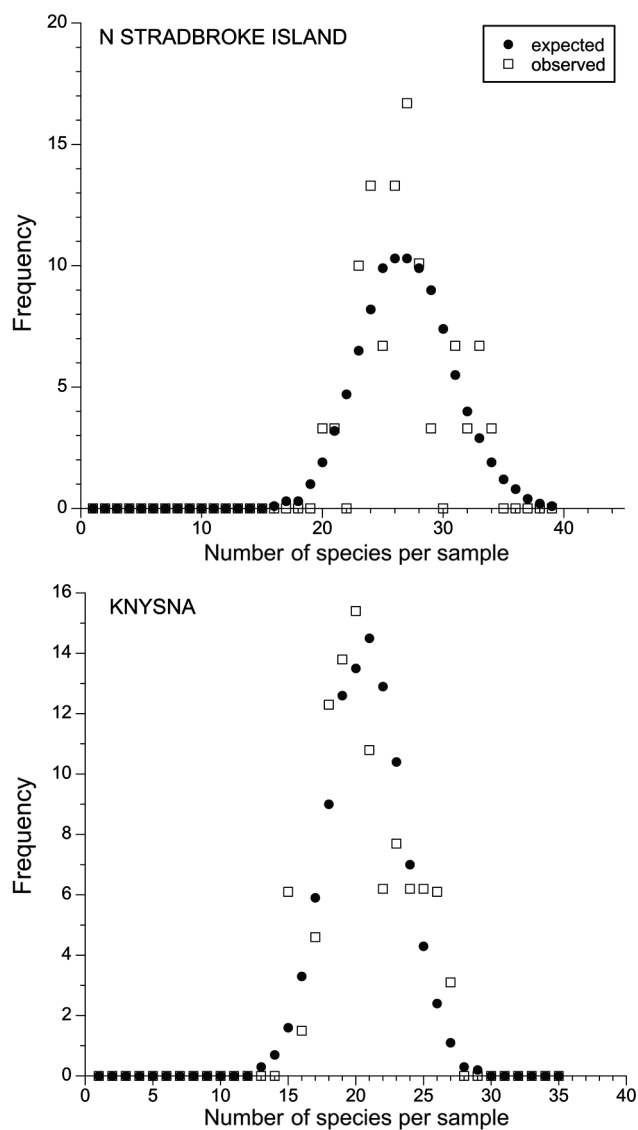
Fig. 2. Similarity of expected and observed frequency of species in 0.0275 m² samples from the seagrass beds in Knysna Bay and on North Stradbroke Island
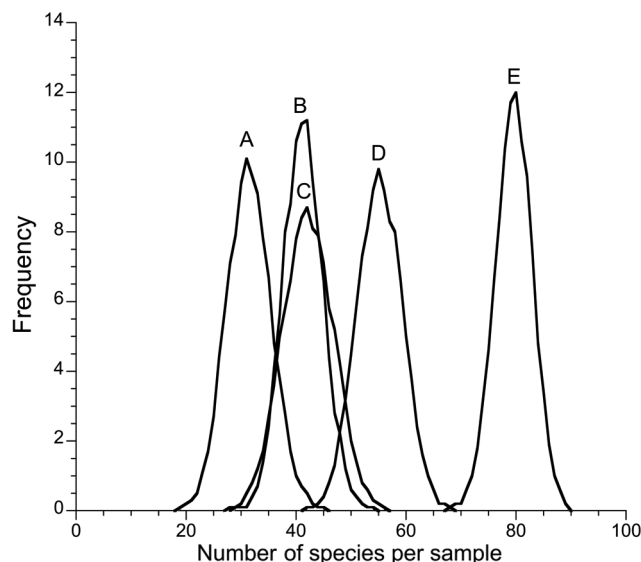

Fig. 3. Expected percentage frequencies of occurrence of different numbers of species per sample (out of a total pool of 100 species in each case) from the 5 ideal frequency of occurrence curves in Jenkins (2011, his Fig. 1), based on the assumption that the species are distributed randomly with respect to each other. (A) Exponential, unimodal with satellite species (sensu Hanski 1982) dominant; (B) sigmoidal, asymmetrically bimodal; (C) normal; (D) linear; (E) exponential, unimodal with core species dominant

Morisita's index of dispersion −0.504; one-tailed p < 0.025), although the actual number expected varies considerably, depending on the shape of the distribution (Fig. 3). Thus, granted the known random assortment of the assemblages in question (Barnes & Ellwood 2011), no further ecological explanation is required for the uniformity of biodiversity in each of the habitat types. This, however, will only push the ultimate explanation of the precise and similar numbers of species per unit area in the different systems, particularly in the seagrass beds, one stage further back to the reasons for the establishment of similar frequency of occurrence curves in the diverse ecological and latitudinal settings in which they occur.

Amongst the many classes of curves proposed by Jenkins (2011) and the other authors cited below, none of whom was concerned with marine or intertidal benthic systems, the general form of the frequency distribution found in seagrass and unvegetated sediment corresponds to the strongly unimodal model of the scheme of Tokeshi (1992), to the unimodal satellite-species-dominant mode in that of McGeoch & Gaston (2002), and to the exponential class of curves in Jenkins (2011). Of the 5 curves in Jenkins (2011, his Fig. 1), this is the one that will yield the fewest expected species per unit area (Fig. 3). Many of the ecological explanations proposed for such curves involve processes operating at the spatial scale of fragmented populations within larger metacommunities, but Collins & Glenn (1997) have suggested that recruitment limitation might produce them locally. Their argument, however, was based on terrestrial species with poor dispersal ability over large spatial scales with consequent limited numbers of recruits to individual local populations, which is clearly inappropriate to the present situation. Nevertheless, although seagrass beds and sandflats may not be likely candidates for supply-side limitation — with young truncatelloid gastropods and many other species settling in densities of 10^5 ind. m^{-2} (Reise

1985, Bachelet & Yacine-Kassab 1987) — successful recruitment to the adult generation is limited through the action of predators (Reise 1985). Jenkins (2011) suggests that the dominant species would be those immune to such predation, although in the cases under consideration here that is most unlikely (Barnes 2014). Why, however, in the likely absence of interspecific competition some species are widespread (and abundant) whilst many others of seemingly equivalent life style and general body form are so rare is not known, although there is often a relationship between a species' geographical distribution and its abundance (Borregaard & Rahbek 2010). Traditionally, zoologists, though less so botanists, have sought to understand assemblage structure in terms of interspecific competition, but other comparative approaches that operate irrespective of whether the carrying capacity is attained are also possible (Götzenberger et al. 2012), including those based on congruence of taxa and of feeding guilds together with other biological traits (Bremner et al. 2003, 2006). Understanding the ecological similarities between that subset of components of, for example, the seagrass assemblages of Moreton Bay, Knysna and Scolt Head most responsible for generating the equivalently shaped frequency of occurrence distributions might go some way to suggesting an answer.

Finally, the above results suggest that assessing variation in numbers of species per unit area may prove a simple and convenient way of estimating the intensity of processes structuring the assemblages concerned: the more the number of species departs from spatial uniformity, the less randomly will they be dispersed, and hence the greater the likely effect of deterministic processes.

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