SMALL-SCALE DISTRIBUTION OF SPECIES RICHNESS IN A GRASSLAND (BÍLÉ KARPATY MTS., CZECH REPUBLIC)

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Abstract: Variation in the number of species was studied in a subthermophilous grassland at a scale of 0.05 × 0.05 m during a 5-year period. The observed variance of species richness (VSR) was compared with a null model based on random distribution of species over a set of squares. It was found that distribution of species richness had more values than expected around the mean and less values at the "shoulders". Both tails fell within the predicted limits. Application of the procedures removing spatial dependence (random shifts, rotation/reflection method by PALMER & VAN DER MAAREL 1995) and environmental heterogeneity (patch model by WATKINS & WILSON 1992) did not change the observed pattern.

Using simulations in which the number of clumps and clumping intensity were manipulated it was found that the effect of the clumped spatial pattern on VSR results in a wide range of variances. Both variance excess and variance deficit were found more frequently than expected under the null model.

To test the effect of the limitation to the number of individuals per square a null model was developed which included the observed number of plant shoots per square, the observed distribution of the number of shoots belonging to individual species per square and the observed spatial distribution of the shoots. The observed VSR was still lower than that produced by the null model. Therefore, it is concluded that at a scale of 0.05 × 0.05 m plant species combine in a non-random way in the studied grassland. It is suggested that the shape of left and right "shoulders" of the species richness distribution may be caused by different factors, such as positive and negative covariance between species, respectively. Their simultaneous impact can generate the observed pattern in species richness.

INTRODUCTION

The complexity of biotic communities makes utilisation of field experiments complicated. Therefore, descriptive and comparative approaches still play a significant role in community ecology. In addition, the structure of natural communities has been studied using comparisons with simulated species assemblages (HARVEY et al. 1983). If a difference between the random and the observed patterns is found, then one investigates for possible mechanisms. Owing to the simplicity of this approach, and difficulties with manipulation in natural communities (WILSON 1995b, AARSSEN & EPP 1990), inferring mechanisms from the observed pattern is quite frequent in community ecology (GREIG-SMITH 1983, JONGMAN et al. 1987).

One of the recently developed methods used for detecting community structure utilises the variance of species richness (VSR) (SCHLTER 1984, PALMER 1987, WILSON et al. 1987). In this approach the observed VSR is compared with the expected one, calculated for randomly distributed species with fixed frequencies.

Forum: Assembly rules, niche limitation and data on pattern
The approach has recently been discussed by Lepš (1995) and Wilson (1995b). They suggested that the null model is not correct because "competition of individuals (genets) for space" (Lepš 1995) and limitation to the number of plant modules (Bycroft et al. 1993, Wilson 1995b) decrease the expected VSR. It has been argued (Watkins & Wilson 1992) that if the number of individuals is usually > 1 the results are not affected. However, Palmer & van der Maarel (1995) showed that the problem persists unless the number of individuals per area is much higher than the species pool. I agree both with Lepš (1995) and Wilson (1995b) that there is, theoretically, a limit to the number of individuals and modules which can fit into a plot. However, it is still unclear whether the above-mentioned limitation plays a role in real plant communities. Based on computer simulations Barta et al. (1995b) suggested that clumping of plants results in a high variance in species richness. Using a different method Palmer & van der Maarel (1995) found that clumping may result in variance both lower and higher than expected.

I tested the effects of spatial pattern of plant individuals and limitation to the number of shoots using real data. For this study I selected a homogeneous species-rich grassland because it has been suggested that the chance to find the variance deficit is highest in this type of community (Wilson et al. 1987, Barta et al. 1995b). Most studies dealing with the VSR at small scales have used data from a single observation or a single season (but see Wilson et al. 1992). Here I utilise 5 years of data from a fixed plot to assess the year-to-year changes.

MATERIAL AND METHODS

The sample plot was established in the National Reserve of Čertoryje in South Moravia, Czech Republic (48°54' N, 17°25' E), in a subthermophilous meadow dominated by Bromus erectus and Carex montana. The area is not fertilized and is mown regularly at the end of June. A detailed description of flora, vegetation and soils can be found in Tlusták (1975), Jongepierová et al. (1994) and Klimeš et al. (1995).

A permanent quadrat (1.5 × 1.5 m) was established on the selected plot in June 1991. The quadrat was divided into 900 squares, 0.0025 m² each, by a cord. In these squares rooted vascular plants were recorded during the second week of June, from 1991 to 1995, usually 1 to 3 weeks before the meadow was cut. From 1993 to 1995 I also recorded the number of individuals, defined as shoots.

The observed VSR was compared with the expected one calculated for the same number of species, randomly distributed over the set of squares, with fixed frequencies (e.g. Wilson et al. 1987). I calculated 2000 randomizations for 2-tailed tests. The differences were interpreted as significant when P < 0.05. The results were expressed as a relative deficit or excess of the VSR (RV[%] = 100 * observed VSR / expected VSR). The 900 squares were merged to 225 (i.e. 4 neighbouring squares merged to form a quadrat), 100, 36 and 25 squares for evaluation of the effect of different scales on RV.

Due to the spatial arrangement of squares in the grid, nearby samples are more similar, on average, than distant samples (Palmer 1987, Palmer & van der Maarel 1995). Therefore, the probability of Type I error is inflated unless spatial dependence is corrected. I used two methods suggested by Palmer & van der Maarel (1995) to remove the effect of spatial dependence. The rotation/reflection method is the only method keeping the original spatial pattern exactly. There are eight possible permutations of the grid data for each species. As