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Variability in species richness within Minnesota oldfields: a use of the variance test

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Abstract

The variance test, originally proposed for testing species associations, is used to test whether species richness is more or less variable than expected under the null model of no species interactions. Species richness is more variable than expected in some fields, and less variable than expected in other fields at the Cedar Creek Natural History Area in Minnesota. High variance in species richness may be caused by variability in competitive exclusion rates or small-scale environmental heterogeneity. Low variance in species richess may occur if the community is saturated with species, or if species-rich areas have high local competitive exclusion rates. Results of the variance test depend somewhat on quadrat size, and can be used to select study sites and quadrat sizes for further research on the nature of variation in species richness.

Introduction

Replicate samples from within a given area generally do not have constant species richness. Even if the environment was spatially homogeneous and species were distributed independently of each other, one would expect some variability in species richness due to chance. An ecologist interested in elucidating the structure of a given community might pose the following question: is the observed number of species per quadrat in a given community more or less variable than one would expect due to chance? If this question can be answered in the affirmative, it would then be worthwhile to ask questions and pose hypotheses about the cause of this small-scale variation in species richness. Alternatively, it would not be as worthwhile for an investigator to seek causes of variability in species richness if species richness is only as variable as we would expect if species were distributed randomly and independently of each other.

The null hypothesis that species richness is as variable as one would expect if species were distributed independently can be statistically tested with the variance test. Although the variance test has been previously proposed as a test for species interactions (Pielou, 1972; Schluter, 1984; McCulloch, 1985), its use as a test for species richness is more direct. The test statistic can be expressed as follows:

$$V = S_o^2 / S_e^2 \qquad (1)$$

where S_o^2 is the observed variance in number of species per quadrat, and S_e^2 is the expected variance in number of species per quadrat. Assuming that species are distributed independently of each other:

$$S_e^2 = \sum_{i=1}^{M} p_i(1 - p_i) \qquad (2)$$

where p_i is the proportion of quadrats containing species i, and M is the total number of species. The expected variance in species richness is merely the sum of the variance of each species' frequency, because the covariance between species according to the null hypothesis is zero (Schluter, 1984). The statistic V from Eq. 1, when multiplied by the number of quadrats (N), is approximately χ^2 distributed with N degrees of freedom (McCulloch, 1985).

Variation in species richness is likely to depend on quadrat size. Very small quadrats include individuals which are directly interacting with each other, i.e. the roots if not the leaves of these plants are probably in close contact. Small-scale dynamics such as those described by Turkington & Harper (1979) may lead to variation in the species richness of these quadrats. However, since small quadrats contain relatively few individuals, measured species richness may be limited by small sample size. Larger quadrats will include more individuals, but they will generally also include individuals which are not directly interacting with each other. Variation in richness in large quadrats might be relatively low because large quadrats share more species than small quadrats. On the other hand, variation in richness in large quadrats might be relatively high, because large quadrats are more representative samples of subregions within a site. We can thus distinguish gradients in environmental variables or community composition correlated with species richness more adequately. Because the scale of interactions between plants is generally unknown, there is no *a priori* reason for an investigator to select a particular quadrat size for the analysis of causes of variation in species richness. If the value calculated by Eq. 1 varies as a function of quadrat area at a given site, the quadrat area for which this value is maximum can be considered the ideal quadrat area for subsequent study of patterns of species richness.

Here, I use the variance test to determine whether species richness within six Minnesota oldfields is more or less variable than one would expect due to the null hypothesis of no species interactions. In addition, I examine the dependence of the results of the variance test on the scale of sampling (i.e. quadrat size).

Methods

In summer 1982, I selected six oldfields for study (hereafter they are named by the last cultivated crop and year of abandonment). All fields were part of the Cedar Creek Natural History Area, except for Maize (1982), which was on adjacent land. Cedar Creek Natural History Area is managed by the University of Minnesota, and is located on a sandy glacial outwash plain in Anoka and Isanti counties, Minnesota. Fifty circular quadrats of each of four sizes (0.01 m^2, 0.1 m^2, 1.0 m^2, and 10.0 m^2) were randomly placed in each field. I recorded the presence of each vascular plant species within each quadrat. The variance test was performed as described above.

Results and discussion

For three of the fields studied (Maize, 1943; Rye, 1965; and Rye, 1971), variance in species richness was much greater than predicted by the null hypothesis of no interspecific interactions, at least for the three largest quadrat sizes (Table 1). Species richness was less variable than expected (for at least some quadrat sizes) in the other fields (Soy, 1955; Rye, 1981 and Maize, 1982). No significant trends were observed for Soy, 1955.

How should these observed patterns be interpreted? The high variance in species richness in some fields could be caused by high dominance of superior competitors in fertile microsites, and lack of competitive exclusion (hence higher species richness) in infertile microsites. Alternatively, some areas within a field can have higher small-scale variability in environmental parameters than other areas; species richness would be quite high in the variable area relative to the more uniform area. Both of these explanations have been previously proposed for patterns of species richness in Cedar Creek olfdields (Tilman, 1982). Many other explanations are possible. Schluter (1984, Table 4) lists several alternative explanations for either positive or negative associations.

Explaining the lower variance than expected in some fields is more difficult. According to Schluter (1984), this condition is 'highly unusual and demanding of further study'. Species could be negatively associated with each other, due to competitive effects. Also, it is possible that in a given site, small-scale species richness is held constant by

Table 1. Observed and expected variance of species richness per quadrat for four quadrat sizes (S_o^2 and S_e^2, respectively) in six Minnesota oldfields. S_e^2 is calculated according to Eq. 2 in the text. Tests of significance are based on the approximate χ^2 distribution of the statistic V (Eq. 1).

Quadrat size (m^2)	Mean species richness	S_o^2	S_e^2	V
Maize 1943				
0.01	3.06	1.81	1.84	0.98
0.10	4.90	5.28	2.90	1.82^{+++}
1.00	7.80	7.01	4.43	1.58^{++}
10.00	11.54	12.95	6.14	2.11^{+++}
Soy 1955				
0.01	5.40	2.45	3.42	0.72
0.10	8.70	3.24	4.52	0.72
1.00	14.16	6.04	6.11	0.99
10.00	18.88	6.35	6.48	0.98
Rye 1965				
0.01	3.52	3.68	1.97	1.87^{+++}
0.10	5.20	5.90	2.43	2.42^{+++}
1.00	7.94	11.77	3.56	3.31^{+++}
10.00	10.90	10.09	4.69	2.15^{+++}
Rye 1971				
0.01	2.46	1.76	1.44	1.23
0.10	5.16	6.95	2.82	2.46^{+++}
1.00	7.00	9.55	2.89	3.30^{+++}
10.00	9.02	6.04	3.23	1.87^{+++}
Rye 1981				
0.01	4.26	1.18	1.82	0.64^{-}
0.10	6.72	1.80	2.15	0.84
1.00	9.50	2.54	2.15	1.18
10.00	12.64	2.56	2.79	0.92
Maize 1982				
0.01	1.80	0.57	0.88	0.65^{-}
0.10	2.36	0.64	1.14	0.56^{--}
1.00	3.48	0.78	1.40	0.56^{--}
10.00	6.60	1.63	2.06	0.79

$^{+}$ Species richness is more variable than expected, $p<0.05$; $^{++}$ $p<0.01$; $^{+++}$ $p<0.001$; $^{-}$ species richness is less variable than expected, $p<0.05$; $^{--}$ $p<0.01$.

negative feedback; i.e. the community is saturated with species. These explanations are not likely to hold for Rye (1981) and Maize (1982), because these fields are young and can not be considered to be in equilibrium (their component species are mostly transient weeds). Low variance in species richness can occur if the environment is uniform (as one might suspect after agricultural abandonment). However, if this alone is the cause of low variance (i.e. there is no interaction between species), observed variance of species richness would be equal to, not less than, the expected variance of species richness.

Within site variation in seed density might also lead to variance in species richness. Areas with high seed densities will generally have more species (as an artifact of high sample size). Once the seeds germinate, these areas will also have a relatively high local extinction rate, because there are more competing seedlings. Areas with low initial seed densities will generally have fewer species and lower extinction rates. These processes are mostly likely important in young fields where chance variation in seed density may be transient, and where processes leading to high variance may take time to develop.

If an investigator is interested in examining intra-community determinants of species richness, the variance test can aid in selection of ideal study site and quadrat size. For example, it might not be fruitful to study determinants of species richness in Soy (1955), because species richness per quadrat in that fields behaves as we would expect by chance. However, species richness in Rye (1965) and Rye (1971) is much more variable than expected by chance. The investigator should use quadrats on the order of 1 m^2 in area because variance in species richness at that scale is threefold the expectation (Table 1).

A note of caution is in order here. An assumption of this (and any other) statistical analysis of quadrat-based data is that quadrats are independent samples of the community. However, quadrats (even randomly placed ones) can be spatially dependent on one another. For example, if species richness is high in a quadrat at a given location, a randomly placed quadrat that happens to be nearby is also likely to have a high species richness. Spatial dependence can cause inferential error which is intensified by increasing sample number (Cliff & Ord, 1981, Chapter 7). For some statistical tests, corrections for this problem have been developed (Cliff & Ord, 1981; Fingleton, 1986). At present, it is unclear how spatial dependence affects the variance test; the statistical inferences in Table 1 should therefore be considered neither exact nor unbiased.

Conclusions

The variance test directly tests whether species richness is more or less variable than expected due to chance. However, it does not distinguish the mechanism (e.g. competition, environmental variability) determining variation in species richness. The variance test can be used to select appropriate study sites and quadrat sizes for further research on the nature of intra-community species richness patterns.

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