

What constitutes evidence of community structure? A reply to van der Maarel, Noest & Palmer

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Abstract. Van der Maarel et al. (1995) - hereafter VNP - criticize our analyses of Öland limestone grassland. They have four general objections, addressed below.

1. VNP attribute our significant results to randomness ('volatility'); however, significant deviation from randomness cannot be explained by randomness. VNP's conclusion of volatility derives from results that are inconsistent with ours. Their ecological interpretation assumes spatial and temporal near-constancy in the vegetation; we demonstrate that these assumptions are not correct.

2. We discussed physical limitations to plant module packing. VNP give estimated module sizes. We appreciate this information, though data on actual module sizes and overlap patterns would be required before the real module packing effects could be determined. If module packing were really the main cause of deficits of variance in richness, the effect would not fluctuate between sites and years, as VNP admit it does.

3. The shape of the richness frequency distribution is a potentially interesting additional form of analysis, albeit one that we had chosen not to include in our analysis. However, it is surprising that VNP dismiss analysis of richness variance, but then interpret a more subtle aspect of the richness distribution - the skewness. VNP's redefinition of the terms 'Niche facilitation' for a deficit of low richness values, and 'Niche limitation' for a deficit of high values, leads them to misrepresent our arguments. They are mistaken in suggesting that niche limitation will necessarily lead to a skewed curve: they do not allow for the fact that the species frequencies, on which the null model is based already, incorporate effects of species interactions. 'Niche facilitation', as defined by VNP, would lead to a variance excess, not a deficit as they assume.

4. VNP's criticism of *a priori* guild classifications had already been met by our use of the intrinsic guild approach. Guild analyses offer the best way forward.

VNP use principally the methodology of 1987. There have been a number of methodological advances since that time. We used these advances in our original paper specifically to circumvent the kinds of problems that they identify. We agree with VNP that it would be very useful to explore the mechanisms behind assembly rules with experiments, but the logical first step is to identify potential assembly rules, as we have been attempting to do. We conclude that, whilst VNP make some interesting observations, none of their criticisms invali-

date our results or conclusions. Our original approach stands as the best known approach, we believe, for searching for community structure in such data, and we reaffirm the validity of our ecological conclusions.

Keywords: Assembly rule; Spatial autocorrelation; Variance in richness.

Introduction

Eddy van der Maarel and colleagues (*i.a.* R.K. Peet, E. Rosén, G. Rusch, M.T. Sykes) have been recording small-scale community pattern in limestone grassland on the Swedish island of Öland. Van der Maarel recommended that we use recently-developed methods to analyse the data for community structure. We did so, and attempted a balanced evaluation of the results (Wilson et al. 1995 - henceforth WSP). Van der Maarel et al. (1995) - henceforth VNP - subsequently performed more detailed analysis of the shape of the richness distributions, which we appreciate. However, in the process they have criticized our approach. It is true that there are always problems of interpretation of 'snapshot' data in terms of community structure (Wilson 1995b). These are discussed in WSP, indeed they have long been recognized in the literature. We believe our approach can provide useful ecological information, and that our interpretations are valid.

We consider VNP's criticism under the four main categories identified in their abstract:

- (1) the occurrence and validity of statistical significance;
- (2) physical limitations to module packing;
- (3) Niche 'limitation' and 'facilitation'; and
- (4) Guild analysis.

The occurrence and validity of statistical significance

Volatility

VNP suggest that our results are due to random fluctuation: “deviations [in variance in richness] are temporary and ephemeral results of local appearances and disappearances of species in small subplots”, “the (random) concentrations of species”. However, WSP demonstrated that there were more significant results than expected on a random basis. This cannot be explained by random fluctuation. VNP note that we found apparent variation in community structure between years. The concept is common in animal ecology (see WSP for references). We see no reason to disbelieve the indication that we found a similar phenomenon in plants.

The conclusion of volatility that VNP reach seems to be caused by two problems with their analyses:

Lumping of fertilizer/irrigation treatments

The quadrats analysed by VNP apparently comprise five or sometimes six different fertilizer/irrigation treatments. VNP lump all these treatments in reporting their analyses. This has the likely consequence of obscuring trends, since WSP found evidence suggesting that the treatments differed in community structure. It is also likely to lead to ‘volatility’, because the first two sampling times represent control vegetation and subsequent ones represent different stages of response to the treatments applied (save in the control quadrats).

The calculations of VNP are problematic

To determine the cause of the ‘volatility’ that VNP report, we calculated RV_r values for all 10-cm² quadrats. For all sites but one, VNP reported more significant variance deficits than are in fact present (Table 1). VNP and we were very careful to ensure that we were using the same version of the data. The few individual RV_r results that VNP report are consistent with our calculations, confirming that the data are the same. However, there are severe discrepancies in the P values. We have thoroughly checked our programming and calculation. Indeed, we have used our programs for ten years, and have checked different programs against each other. We are confident that our calculations are correct. We are therefore at a loss to explain why their values are different from ours.

Conclusion

VNP’s dismissal of our significant results as due to randomness was probably caused by the lumping of treatments and by problems with their calculations.

Assumptions of homogeneity

Much of VNP’s ecological interpretation is based on an assumption of spatial and temporal near-homogeneity in the Öland grassland. They use this assumption to dismiss our significant results, apparently on the basis that if our results differ from their concepts, the results must be wrong. For example, they dismiss our significant results as “capricious”, “a result of random fluctuations”, and “temporary and ephemeral”, and they use homogeneity as a reason for dismissing the concept of life-history guilds. Homogeneity is the basis for their conclusion that cases of $RV_r > 1.0$ are due to: “(random) concentrations of species in temporarily favourable microsites ...”. We examine three aspects of this assumption of homogeneity:

Spatial heterogeneity: differences between quadrats

VNP state that “alvar grassland is floristically homogeneous”. I.e., the probability of occurrence of a new species is pretty much consistent across all quadrats. Our interpretation is that there are microsite differences. We tested between these two interpretations by using (separately for each site) a four-dimensional DCA ordination (for those blocks which were recorded through all five years, using data for 10-cm² quadrats. In this analysis, the attributes were the species, and the records were the quadrats × years combinations (normally 50 quadrats × 5 years = 250 combinations), entered into the analysis with no information on which record was from which quadrat or year. We then performed a quadrats × years analysis, to test for differences in DCA score between quadrats and between years (testing those against the quadrat year interaction), i.e. to see whether particular quadrats and years had with some consistency separated out in ordination space.

There were significant differences between quadrats on all four axes in all three sites (Table 2a). This could be because of environmental patchiness, or because of a tendency for perennials to persist, either way disproving

Table 1. Significant deviations of variance richness from a null model, 10-cm² quadrats. VNP = values reported by VNP. Recalc. = recalculated by us from the same data.

	Excess of variance		Deficit of variance	
	VNP	Recalc.	VNP	Recalc.
Gettlinge 1	1	1	13	8
Gettlinge 2	2	2	6	3
Gettlinge 3	0	0	4	0
Kleva	1	1	8	4
Skarpa Alby	0	0	11	6
Total	4	4	42	21

Table 2. Analysis of variance on D.C.A. ordination scores. F = variance ratio; P = probability under the null model.

	Dimension							
	1		2		3		4	
	F	P	F	P	F	P	F	P
(a) Differences between quadrats								
Gettlinge	7.5	0.000	7.0	0.000	7.5	0.000	5.9	0.000
Kleva	7.5	0.000	5.6	0.000	5.4	0.000	4.6	0.000
Skarpa Alby	7.6	0.000	7.8	0.000	4.5	0.000	3.3	0.000
(b) Differences between years								
	F	P	F	P	F	P	F	P
Gettlinge	11.9	0.000	2.4	0.051	2.5	0.045	0.4	ns
Kleva	38.9	0.000	0.9	ns	9.6	0.000	20.7	0.000
Skarpa Alby	1.9	ns	3.7	0.006	0.9	ns	1.0	ns

VNP’s assumption of spatial homogeneity, and supporting our interpretation of microsite differences.

Temporal heterogeneity: differences between years

VNP suggest there are “no big changes in ... species frequency over the years”. In the ordination described above, there are significant differences between years in one or more axes for all three sites (Table 2b). VNP’s assumption of temporal heterogeneity is not supported by the data.

Differences between quadrats and years in species richness

VNP agree that ‘favourable’ and ‘unfavourable’ microsities are both present, but they suggest that such differences are temporary (e.g. “temporally [*sic*] favourable microsities”). However, our analyses (Table 6 of WSP) demonstrated that there is considerable (and highly significantly) consistency between years in which quadrats are species-rich and which are species-poor.

VNP also claim that there is little difference between years in species richness, e.g.: “there are no big changes in species richness ... over the years”. However, we had already demonstrated yearly variation in species richness (Table 3 of WSP), for example, at Gettlinge there was a mean of 4.5 species per quadrat in 1993 and 8.4 in 1988, the latter almost double the former, and this variation was highly significant.

Conclusion

VNP’s assumption of spatial and temporal near-homogeneity of the vegetation was based on their observations of variation between the 50 (or so) quadrats within a site/block. Our analyses have been conducted at the same spatial scale. It would be dangerous to dismiss our significant results just because they conflicted with VNP’s assumption of spatial and temporal

homogeneity. It is even less valid when, as we have demonstrated at the same spatial scale, that assumption is incorrect.

Spatial autocorrelation (SAC)

VNP say that SAC “may affect richness variance”. As Palmer & van der Maarel (1995) make clear, SAC itself has no tendency to increase or decrease richness variance. What SAC does is to affect estimates of the significance (i.e. the P value). VNP say “corrections for this dependence should be made”; we had done this by using a patch model (Wilson 1995).

VNP claim that “More than half of the significant cases become nonsignificant” [after correction for SAC], later “The number of significant deviations from $RV_r = 1$ is reduced by more than 50%”. In fact the reduction is by 44% (14 out of 32). We too found fewer significant cases when we used a patch model, which corrects for SAC (and also removes most effects of environmental heterogeneity). Moreover, it is of little consequence that 44% of VNP’s variance deficits should become nonsignificant when analysed by the Reflection method, since 50% of the cases of significance that they report appear to have been spurious in the first place (Table 1). It is surprising that the Reflection method did not remove *more* significances.

Conclusion

SAC is indeed present in the data. The Reflection method will remove its impact very effectively (Palmer & van der Maarel 1995). However, the apparently loss of significance reported by VNP is primarily because many of their significances were spurious, artefacts of their calculations. The patch models, that we used, are conservative in the face of autocorrelation, *and* allow for environmental heterogeneity.

Physical limitations to plant module packing

VNP say: “We suggest that there may be a simple physical limitation”. In interpreting a deficit of variance, Wilson and colleagues have always acknowledged, and often evaluated, this possibility (Watkins & Wilson 1992; Wilson et al. 1992; WSP). VNP attempt to quantify this effect, giving for 44 species the estimated modal size (it is not clear whether or not any measurements were involved) of of “individuals (plant units)”. They then take into account that several such units may occur together (spatial aggregation), and on the other hand that species may be present in different strata (cf. Roxburgh et al. 1992). However, this ignores that van der Maarel and colleagues recorded *shoot* presence, so: (a) the unit of shoot presence is the module, for most species a single leaf or leaflet; and (b) it is necessary for only a small fraction of a module to be in the quadrat for it to be counted.

To assume that one explanation has priority until absolutely disproved does not seem to us useful. It seems a better approach in science to consider all possible explanations, to assess the prior likelihood of each, and to use the results of an investigation to refine those likelihoods (Wilson 1995b). To determine the likelihood of module packing effects, we would need data on actual distributions of module sizes, and detailed information on the patterns of module overlap. If a physical limitation to module packing really is the main explanation of low RV_r , why is the effect, as VNP admit, intermittent in time and space? Deviations from the null model cannot be a “temporary and ephemeral” “result of random fluctuations in species number” and also be an inevitable consequence of module packing.

Conclusion

It is unlikely that there is only one process operating. Probably, several processes are occurring simultaneously, as is almost always the case in ecology. Limitations to module packing undoubtedly occur. We attempted a balanced consideration of this effect. We do not feel that VNP’s consideration adds to, or detracts from, our results.

Niche limitation and ‘facilitation’

VNP use the symmetry of the richness distribution to criticize our ecological interpretations, and to make their own.

Skewness of richness

VNP claim that we have missed information by ignoring the skewness of the richness distribution. The calculation of skewness by VNP is interesting, but we question its utility. Interpretation of variance in richness is not unambiguous (Watkins & Wilson 1992; Bycroft et al. 1993; Palmer & van der Maarel 1995a; Wilson 1995a, b). How much more difficult would be ecological interpretation of the higher moments such as skewness! It is strange that VNP believe that “it would be possible to differentiate between ‘niche limitation’ (significantly left-skewed), ‘niche facilitation’ (significantly right skewed) ... “, when they do not believe it is possible to draw conclusions on community processes from such data at all (“these rules cannot be detected through the kind of spatial analysis described in this and related papers”).

VNP, throughout, confuse the interpretation of a deficit of variance by assuming that a deficit of richness

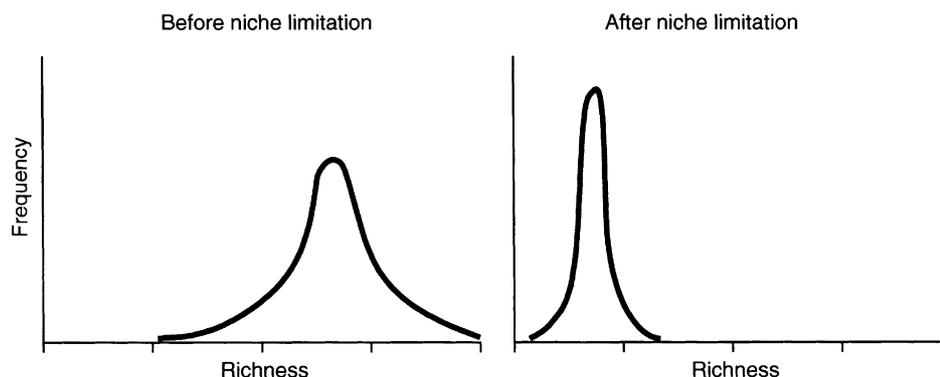


Fig. 1. Theoretical distribution of richness values before and after niche limitation.

values to the left of the observed mean will imply 'niche facilitation' (a requirement for certain species to be established immediately after a disturbance before certain other species would develop) and one to the right will imply niche limitation. Such an interpretation was not proposed by us, the original use of 'niche limitation' in this context referred to a process that would lead to a deficit in both high and low values. VNP's usage has not been proposed by anyone else in the literature. If it is VNP's own interpretation, then it is disproved by their own argument: if niche facilitation were occurring, there would be some quadrats where the facilitator had not arrived and which were therefore empty; as VNP admit, such quadrats are almost absent. Such a deficit of low-richness quadrats can be explained most simply by colonization, which VNP admit is fast: "in many cases ... the invasion goes faster than expected".

Behind all this is a serious misunderstanding. VNP compare the observed distribution of richness with the null-model distribution, as if the latter were the distribution one would find if there were no interactions between species. However, the null-model distribution is based on the species frequencies observed *after* any interactions have occurred. The potential distribution of species frequencies, and hence of quadrat richnesses, were there no such interactions, is unknown. It is possible that because of niche limitation *every* quadrat has a lower richness than it would obtain in the absence of species interactions (Fig. 1).

We conclude that a deficit of low-richness sites is much more likely to be due to colonization than to 'niche facilitation'. The analysis of skewness is potentially interesting, but it does not bear on the validity of our conclusions. It is clear that niche-limitation theory (e.g. MacArthur & Levins 1967; Abrams 1990) predicts a trend towards lower variance in richness, but ecological utility in separating 'left and right deficits', or of analysing the shape of the distribution, has yet to be demonstrated.

Variance in richness

VNP suggest that 'niche facilitation' can cause a variance deficit. However, either:

- a. Facilitation occurs in all quadrats with equal readiness. In this case there is no effect on the variance between quadrats - facilitation is just part of the colonization process. Or:
- b. Facilitation occurs in some quadrats, but not others. In this case there will be some quadrats with few species where the facilitator(s) has not arrived, and others with many species where it has. This will lead to a *high* variance in richness between quadrats, not a low one.

We have performed simulations which demonstrate this effect. Thus, for example, the RV_r of 0.57 (quadrat

G2-6 in 1989) cannot be interpreted as suggesting "the existence of niche facilitation", as VNP suggest. Any 'niche facilitation' would lead to RV_r *greater* than 1.0, not to a low variance.

Conclusion

VNP's use of the terms 'facilitation' and 'limitation' leads to confusion. WSP analysed for the effects of limitation in both tails jointly, stating *no* expectation, either from theory and from previous results, of asymmetrical curves. Indeed, VNP found: "a majority of symmetrical curves". We appreciate that other authors may prefer different definitions of terms from the original ones, but the problem is that VNP insist on evaluating our statements about niche limitation as if we used their one-tail definition. Moreover, niche 'facilitation' will lead to a high variance in richness, not a low one. Thus, we see no valid basis for the conclusion of VNP: "niche limitation may occur in alvar grassland, but indications for niche facilitation are stronger".

Guild analysis

Guild analyses offer potentially the best solution to the problems with analysing richness that VNP reiterate (Lepš 1995). We believe we used the most sophisticated analyses available. Indeed, VNP suggest no alternatives. In particular, the Wilson & Roxburgh (1994) intrinsic guild approach has solved the problems, reiterated by VNP, of *a priori* guild approaches.

Overall conclusion

Analysis of community structure by comparison with null models looks deceptively simple, but there are many potential pitfalls - in selection of methods, programming, and interpretation of results - which have to be avoided before ecological interpretation can begin. We agree with VNP that it would be very useful to explore the mechanisms behind assembly rules with experiments, but the logical first step is to identify potential assembly rules. That is precisely what we have been attempting to do.

In their analyses, after briefly (in their Table 3) using the Reflection method of Palmer & van der Maarel (1995), the methods of VNP are basically those of Wilson et al. (1987). VNP's criticisms of these methods have already been anticipated and addressed by methodological advances which WSP employed, such as:

- (1) patch models (Watkins & Wilson 1992; Bycroft et al. 1993; Wilson 1995a), which minimize the effect of environmental heterogeneity and of spatial autocorrelation;

(2) summation of within-site variation (Wilson et al. 1992), to maximize the power of the test;

(3) analysis of temporal variation in richness (WSP), to remove the problem of site differences in environment;

(4) guild proportionality analysis (Wilson 1989), to remove the effects of spatial limitations to total richness by holding quadrat richness in the null model equal to that observed; and

(5) determination of intrinsic guilds (Wilson & Roxburgh 1994).

We welcome discussion of our results. However, none of the criticisms of VNP invalidate our results or our conclusions.

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