

Interpretation of scale in paired quadrat variance methods

Guo, Qinghua^{1*} & Kelly, Maggi^{1,2}

¹Department of Environmental Science, Policy and Management, 151 Hilgard Hall #3110, University of California, Berkeley, CA 94720-3110, USA; ²E-mail mkelly@nature.berkeley.edu;

*Corresponding author; E-mail gqh@nature.berkeley.edu

Abstract

Question: Previous interpretations of the variance plot of paired quadrat variance method (*PQV*) have been incomplete. The objective of this study was to clarify the interpretation of *PQV*, and to shed additional light on how different quadrat variance methods can be used, in concert, to measure scale in transect data.

Methods: We used artificial and real data to examine how the *PQV* method elucidates spatial pattern. Two-term local quadrat variance (*TTLQV*) and new local variance (*NLV*) methods, together with their three-term counterparts, were also applied to the same data sets, and the results from all methods were compared.

Results: When the mean gap size equalled the mean patch size along a transect, the first peak of the variance of *PQV*, *NLV* and *TTLQV* corresponded with the gap size (or patch size). However, if the mean gap size and patch size were unequal, the variance plot of *PQV* displayed a flat-topped plateau, in which the first inflection represented the mean size of the smaller phase and the second inflection represented the mean size of the larger phase; *TTLQV* showed a clear peak and *NLV* displayed a distinct first peak while the second inflection was dampened. The results also indicated that the three-term versions of quadrat variance methods did not consistently outperform their two-term counterparts, and often confused the interpretation of scale.

Conclusions: The quadrat variance methods associated with the patch-gap measurements were able to efficiently detect not only the size of patches, but also the size of gaps.

Keywords: Gap; Local quadrat variance; Patch; Spatial pattern; Transect; Three-term quadrat variance.

Abbreviations: *NLV* = New local variance; *PQV* = Paired quadrat variance; *RPQV* = random paired quadrat variance; *TQV* = Triplet quadrat variance; *TTLQV* = Two-term local quadrat variance; *3TLQV* = Three-term local quadrat variance; *3TNLV* = Three-term new local variance.

Introduction

Ecologists have used spatial analysis to detect patterns in plant communities to better understand the distribution of plant species and their relationship to environmental factors. Dale (1999) gives a comprehensive review of the different spatial analysis methods commonly used in plant ecology. There are many spatial analysis methods that are designed for use with mapped point patterns. For example, Ripley's *K* (1976) is highly recommended as an efficient way to detect spatial patterns (Bailey & Gatrell 1995). Ripley's *K*, however, requires a complete census of all individuals in a study area, which can make it difficult to apply in the field (Lepš 1990). Because of this difficulty, ecologists and biogeographers often use transect data to study plant distribution (Wilson & Gurevitch 1995; Akashi 1996; Ma et al. 2001). For transect data, quadrat count approaches, such as two-term local quadrat variance (*TTLQV*), paired quadrat variance (*PQV*) and new local variance (*NLV*), are often applied to examine spatial patterns in plant communities (Hill 1973; Usher 1983; Carter & O'Connor 1991; Schaefer 1993; Ver Hoef et al. 1993; Edwards et al. 1996; Dai & van der Maarel 1997; Dale 1999; Ribeiro & Fernandes 2000).

With these methods, when the quadrat variances are plotted against block size, the peaks of these graphs are interpreted as the scale of the mapped phenomena. For example, the peak value of variance plot of *TTLQV* indicates the mean size of patches and gaps (Dale & MacIsaac 1989), while for the *NLV*, it represents the mean size of the smaller phases (gaps or patches) (Dale 1999). Among various quadrat variance approaches *PQV*, originally developed by Ludwig & Goodall (1978), is commonly used to study the spatial pattern of transect data (Carter & O'Connor 1991; Yang et al. 1991; Schaefer & Messier 1994; Dale et al. 2002; Perry et al. 2002) and is believed to be an effective way to detect the scale of patterns (Ludwig & Goodall 1978; Carpenter & Chaney 1983; Carter & O'Connor 1991). However, the previous interpretations of the peak of *PQV* variance on a variance spacing distance

plot are incomplete. There are two common existing explanations of these peaks on a *PQV* plot. First, Carpenter & Chaney (1983) used simulated transects and demonstrated that the first peak of the variance plot in random paired quadrat variance (*RPQV*) represented the mean patch size. *PQV*, which is based on all possible pairs of quadrats, provides a more accurate detection of patch size than *RPQV*, which is based only on the randomly selected pairs of quadrats without replacement (Ludwig & Reynolds 1988). Second, Dale & Mah (1998) believed the peak of variance in a *PQV* plot indicated the mean distance between the centre of a patch and the centre of a gap. We find that these interpretations are incomplete. Based on real and simulated data, we seek to further clarify the interpretation of the *PQV* variance plot. We are particularly interested in the interpretation of *PQV* and its relationship to patch and gap sizes. *TTLQV* and *NLV* are considered to be efficient ways to detect the scale of patterns, and their characteristics have been well studied (Hill 1973; Galiano et al. 1987; Dale 1999). We apply *TTLQV* and *NLV* to the same simulated and real data sets to better understand the characteristics of *PQV*, and to evaluate how those measures might be used in concert. Meanwhile, since the three-term versions of quadrat methods are commonly recommended (Lepš 1990; Dale 1999), we have also compared three-term local quadrat variance (*3TLQV*), three-term new local variance (*3TNLV*) and triplet quadrat variance (*TQV*) with the results from their two-term counterparts.

Simulated data set

Transect data are often recorded in two ways: presence/absence and density. In this study, we simulated both types of data as follows (Table 1); for presence/absence data, we used 1 and 0 to represent patches and gaps respectively (Carpenter & Chaney 1983; Dale 1999). To understand the effects of various combinations of patches and gaps on the results of *PQV*, we simulated a series of patterns by changing the ratio of patches to gaps. We used two types of simulated presence/absence patterns. The first group (transects a, b and c) were transects with fixed cycle lengths of 12 units which contained fixed-size patches alternating with fixed sized gaps. The second group (transects d and e) consisted of transects with fixed patches (gaps) alternating with random gaps (patches) so that the stochastic effects were considered. We then simulated density data with patches having higher density than the gaps. We generated fixed size patches (the density value was randomly generated ranging from 10 - 15, with a fixed length of 4) alternating with fixed size gaps (the density value was randomly generated rang-

ing from 0 - 5, with a fixed length of 8) (transect f). To evaluate the effect of trends on the density data, we generated a trend transect by combining the transect f with a trend along the transect (transect g). Meanwhile, we also examined the response of quadrat methods to multi-scale transects. The simple additive combination method was used to generate multiscale transects (Lepš 1990; Dale 1999). Both multiscale transect h and transect i were generated by combining two single-scale transects with different patch and gap sizes. The major differences between transects h and i are: transect h combined two transects with the same fixed length cycles (patch + gap = 50), while transect i aggregated two transects with different fixed length cycles (i.e. one with 30 and the other with 50). Each simulated transect consisted of 1000 quadrats. All figures were plotted at block size/spacing distance less than 10% of the total transect length, as recommended by Ludwig & Reynolds (1988).

Existing sample data set

To compare our results with those from other researchers, we used two existing sample data sets from Ludwig & Reynolds (1988). They used *TTLQV* and *PQV* to detect the spatial pattern of two transects. The first transect represents the count of sparrow nests in desert shrubland along a 2600-m transect that is 10 m wide in 10-m sections, resulting in 260 quadrats. The second transect counts the number of fire ant hills in a pasture along a 1280-m transect that is 10 m wide in 10-m sections, resulting in 128 quadrats. Analysis and discussion in the following sections refer to the quadrat size rather than the actual distance.

Table 1. Simulated transects. a, b and c: fixed cycle at 12 (patch size + gap size); d and e: fixed phases (gap or patch), alternating with random phases (patch and gap); f: density transect with the fixed patch and gap sizes; g: the transect f added with a trend along the transect; h and i: multi-scale transects.

Simulated transect	Patch size	Gap size
a	4	8
b	5	7
c	6	6
d	4	Random from 1 to 20
e	Random from 1 to 20	35
f	4 (density)	8 (density)
g	4 (density with trend)	8 (density with trend)
h	4 and 12 (multiscale)	46 and 38 (multiscale)
i	7 and 12 (multiscale)	23 and 38 (multiscale)

Methods

We calculated PQV , NLV , $TTLQV$ and their three-term counterparts TQV , $3TNLV$, $3TLQV$ for the simulated transect data and the existing data sets. All analyses were performed using our Visual Basic programs, which are available to readers upon request. The formulas below are based on Dale (1999).

Paired quadrat variance (PQV) is defined as:

$$PQV(r) = \sum_{i=1}^{n-r} (x_i - x_{i+r})^2 / 2(n-r) \quad (1)$$

Triplet quadrat variance (TQV) is defined as:

$$TQV(r) = \sum_{i=1}^{n-2r} (x_i - 2x_{i+r} + x_{i+2r})^2 / 4(n-4r) \quad (2)$$

New local variance (NLV) is defined as:

$$NLV(r) = \sum_{i=1}^{n-2r} \left| \left(\sum_{j=i}^{i+r-1} x_j - \sum_{j=i+r}^{i+2r-1} x_j \right)^2 - \left(\sum_{j=i+1}^{i+r} x_j - \sum_{j=i+r+1}^{i+2r} x_j \right)^2 \right| / 2r(n-2r) \quad (3)$$

Three-term new local variance ($3TNLV$) is defined as:

$$3TNLV(r) = \sum_{i=1}^{n-3r} \left| \left(\sum_{j=i}^{i+r-1} x_j - 2 \sum_{j=i+r}^{i+2r-1} x_j + \sum_{j=i+2r}^{i+3r-1} x_j \right)^2 - \left(\sum_{j=i+1}^{i+r} x_j - 2 \sum_{j=i+r+1}^{i+2r} x_j + \sum_{j=i+2r+1}^{i+3r} x_j \right)^2 \right| / 8r(n-3r) \quad (4)$$

Two-term local quadrat variance ($TTLQV$) is defined as:

$$TTLQV(r) = \sum_{i=1}^{n+1-2r} \left(\sum_{j=i}^{i+r-1} x_j - \sum_{j=i+r}^{i+2r-1} x_j \right)^2 / 2r(n+1-2r) \quad (5)$$

Three-term local quadrat variance ($3TLQV$) is calculated as:

$$3TLQV(r) = \sum_{i=1}^{n+1-3r} \left(\sum_{j=i}^{i+r-1} x_j - 2 \sum_{j=i+r}^{i+2r-1} x_j + \sum_{j=i+2r}^{i+3r-1} x_j \right)^2 / 8r(n+1-3r) \quad (6)$$

where X_j is the density of the j th quadrat, n is total number of quadrats, r for PQV and TQV represents the spacing distance between two quadrats of interests, while r for the NLV , $3TNLV$, $TTLQV$ and $3TLQV$ is the block size. From the above formulae it is clear that quadrat variance methods are unable to differentiate between patches and gaps. Instead, features identified by these methods represented the size of the larger phase/smaller phase or the average size of the gaps and patches (Dale 1999).

First, we used the PQV , TQV , $TTLQV$, $3TLQV$, NLV and $3TNLV$ with the simulated transect data with known patch and gap sizes. Next, we performed the same analysis on the existing real data sets, in which the patch and gap sizes of transects are unknown. To further validate the results of PQV on these real data sets, we applied two methods proposed by Dale & MacIsaac (1989) to detect the mean gap and patch size. One

approach can be referred to as ‘direct patch-gap measurement’, which uses the mean quadrat density of the transect as a threshold to define gaps and patches. In this method, when the density of a quadrat is greater than the mean density of all quadrats, the quadrat is considered to be a patch, otherwise a gap. The mean patch (or gap) size is then computed, based on the total length of the patches (or gaps) and the number of the segments of the patches (or gaps). The second approach called ‘patch-gap analysis’ ranks the density of the quadrats and is based on the null hypothesis that all rankings have the same probability. A plot of the index of W_k or Y_k is used to interpret the gap size or patch respectively. Detailed formulas of W_k and Y_k refer to Dale & MacIsaac (1989). It should be noted that the patch-gap analysis is problematic for presence/absence data since the method requires the data be ranked. In this case, direct patch-gap measurement or other spatial transect methods (Cowling 1998) could be used in conjunction with quadrat variance methods to reveal the patch and gap sizes.

Results

Simulated data

Presence/absence transects

Fig. 1 shows the results of variance vs block size/spacing distance for the simulated presence/absence transects (transects a, b, c, d and e). When patch size is 4 and gap size is 8 (Fig. 1a), the peak value of NLV was 4. The shoulder of the peak value (right hand side of the first peak value) is often neglected in interpretation of NLV . In this study, the shoulder value represents the mean size of the larger phase in all the simulations. For example, Fig. 1a shows that the shoulder value is 8, which is the mean size of gaps but in Fig. 1c, there is only one peak value at 6, because the gap size equals the patch size. For all transects (transects a, b and c) with fixed gap and patch size, the peak value of $TTLQV$ was 5, while the variance plots of $3TLQV$ and TQV peaked at 6 (Fig. 1 a, b and c). It is well known that there is a peak shift in $TTLQV$ (Dale & Mah 1998) and we observed the peak value of 5 instead of 6 in $TTLQV$. $3TNLV$ had peak values at 6 for transects a and c (Fig. 1a, c) and a peak value at 5 and a shoulder at 6 for transect b (Fig. 1b).

The shape of the PQV variance plot shows several plateaus (Fig. 1a, b). In Fig. 1a, the first inflection of the plateau is 4, the second inflection is 8, which corresponded well with the pattern of transect a in which patch size is 4 and gap size 8. Similar results were also found in transect b (Fig. 1b). The PQV variance plot displays a distinct peak when the mean size of patches equalled that of gaps (Fig. 1c). Since PQV cannot

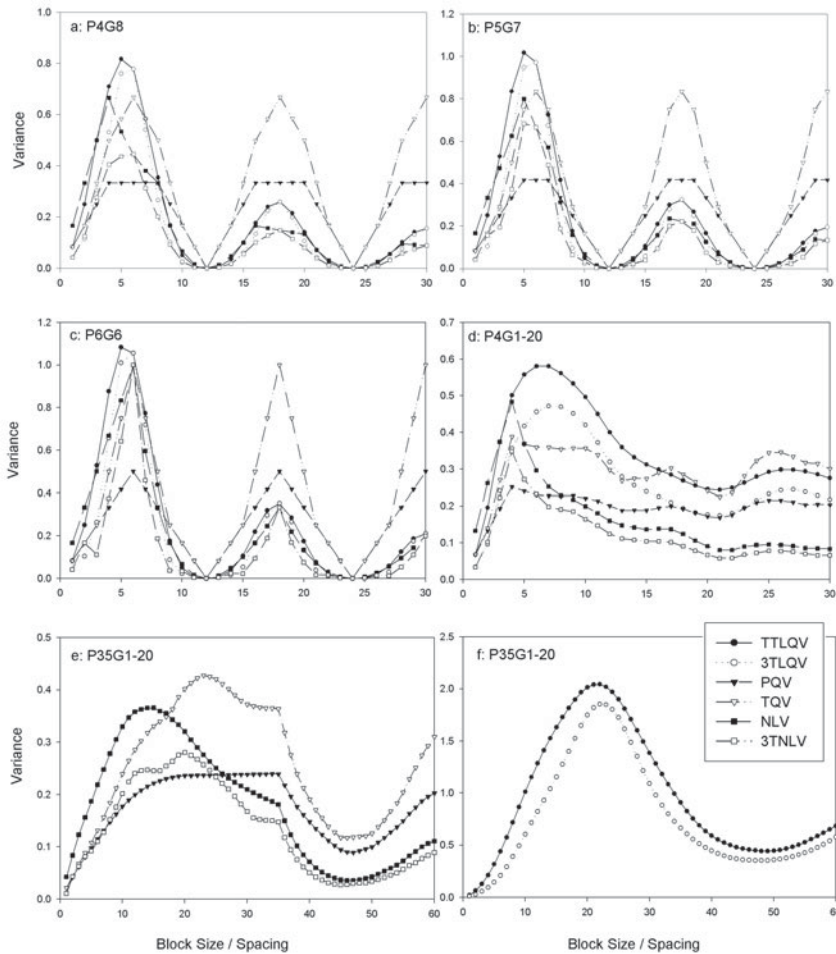


Fig. 1. Variance plots of *TTLQV*, *PQV*, *NLV*, *3TLQV*, *TQV* and *3TNLV* for simulated presence/absence transect data. P = patch size and G = gap size. (a) transect a; (b) transect b; (c) transect c; (d) transect d; (e) *PQV*, *NLV*, *TQV*, *3TNLV* for transect e; (f) *TTLQV* and *3TLQV* for transect e.

distinguish between patches and gaps, it is important to note that the first inflection of the plateau in *PQV* represents the mean size of the smaller phase (either gap or patch) and the second inflection indicates the mean size of the larger phase.

The results from the second group of simulated transects are plotted in Fig. 1d-f, showing the combined effects of fixed patches (gaps) and random gaps (patches). Since none of the methods can distinguish between gaps and patches, we refer to smaller phases and larger phases in the following description. Fig. 1d represents the fixed smaller phases (patches) at 4 with the random larger phases (gaps) which vary from 1 to 20. The mean of random larger phases was ca. 10. Therefore, the mean distance between patches and gaps is 7, which is clearly shown in *3TLQV*. The plot of *TTLQV* displayed a peak value at 6. *PQV*, *NLV*, *TQV* and *3TNLV* all distinctly showed the first inflections or peaks at 4, which are easier to discern compared to the second inflections at

10 (the random larger phases). In addition, *PQV* and *TQV* showed clearer second inflections than *NLV* and *3TNLV*. In contrast to transect d, transect e represents the fixed larger phases (gaps) with the random smaller phases (patches). We plotted *3TLQV* and *TTLQV* (Fig. 1f) separately from other quadrat variance methods (Fig. 1e), as the variances of *3TLQV* and *TTLQV* are much larger than those of other quadrat variance methods. Plots of *PQV*, *TQV*, *NLV* and *3TNLV* (Fig. 1e) showed obscure first peaks at 10 but sharp second inflections at 35, which corresponded well with the patterns in which the random smaller phases (randomly varying from 1 to 20) alternated with the clear larger phases (with fixed size 35). *TQV* and *3TNLV* also showed small peaks at around 22, which corresponded to the mean distance between patches and gaps. The mean distances between patches and gaps were also easy to identify in the *TTLQV* and *3TLQV* plots (Fig. 1f).

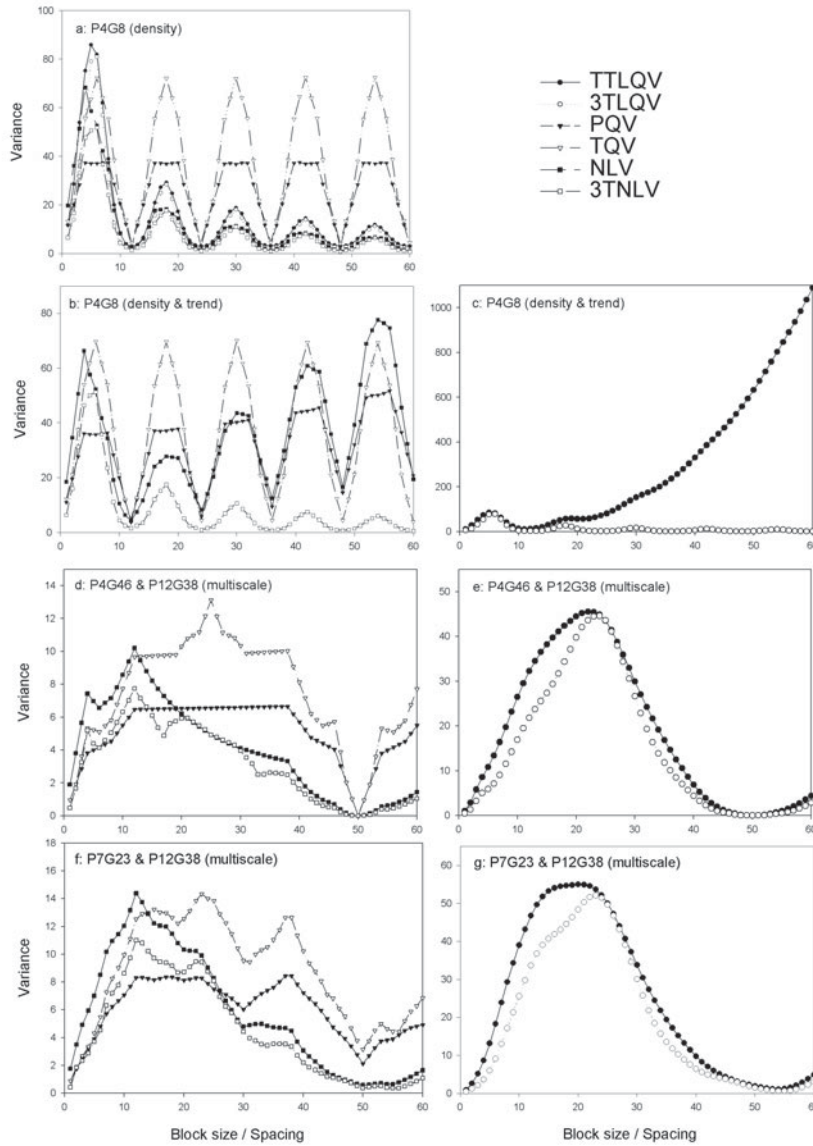


Fig. 2. Variance plots of *TTLQV*, *PQV*, *NLV*, *3TLQV*, *TQV* and *3TNLV* for simulated density data. P = patch size and G = gap size. (a) transect f; (b) *PQV*, *NLV*, *TQV*, *3TNLV* for transect g; (c) *TTLQV* and *3TLQV* for transect g; (d) *PQV*, *NLV*, *TQV*, *3TNLV* for transect h; (e) *TTLQV* and *3TLQV* for transect h; (f) *PQV*, *NLV*, *TQV*, *3TNLV* for transect i; (g) *TTLQV* and *3TLQV* for transect i.

Density transects

Density data showed similar results. The plot of single-scale density transect f (Fig. 2a) displayed similar patterns to that of presence/absence transect a (Fig. 1a). For the trend transect (Fig. 2b, c), the two-term quadrat variance methods (*TTLQV*, *NLV* and *PQV*) responded to the presence of a trend, and exhibited increasing variances over the block size or spacing distance. In particular, *TTLQV* appeared to be very sensitive to trends and increased dramatically after block size 20. In contrast to the two-term variance methods, all three-term counterparts displayed stable variances in

the presence of trends and revealed the similar pattern as shown in Fig. 2a. It should be noted that although the trend affected the variance plots of *TTLQV*, *NLV* and *PQV*, the scales of pattern or sizes of patch/gap were still clearly observable.

For the multiscale transects, Fig. 2d showed the variance plots of transect h which combined two single-scale transects with the same fixed cycle length of 50. *PQV*, *TQV*, *NLV* and *3TNLV* clearly identified various phase sizes at 4, 12, 38 and 46. There were, however, some slight differences among the effectiveness of these methods in distinguishing phase sizes. For example, the

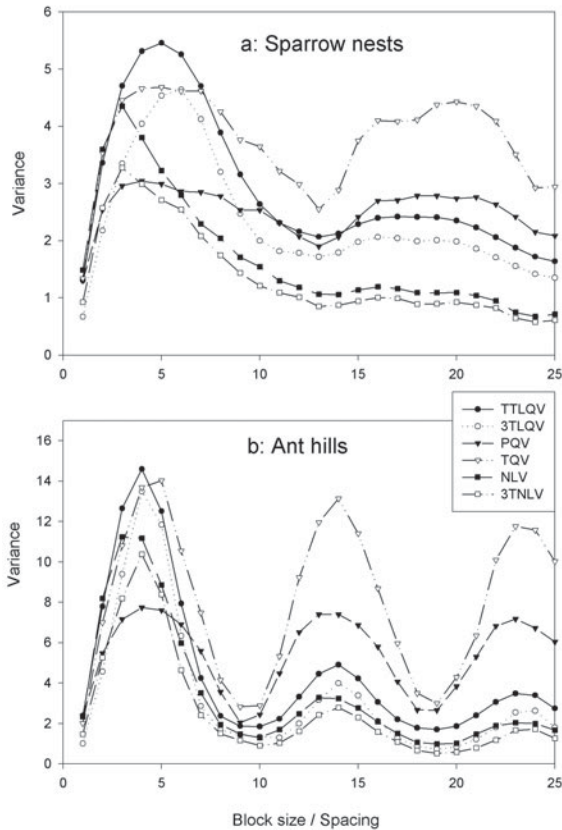


Fig. 3. Variance plots of *TTLQV*, *PQV*, *NLV*, *3TLQV*, *TQV* and *3TNLV* for Ludvig's dataset: (a) sparrow nests in desert shrubland; (b) fire ant hills in pasture.

first and second peaks of *NLV* were more obviously detectable than those in *PQV*; however, the third and fourth inflections of *PQV* were easier to identify than those in *NLV* (the fourth inflection of *NLV* was almost unobservable). *TQV* not only revealed various phase sizes but also showed a distinct peak at 25, which represented the mean distance between patches and gaps. Although *3TNLV* responded to various phase sizes, it displayed less distinct structure than *TQV*, and produced some minor fluctuations which did not match well with any known patterns. Compared to *PQV*, *NLV*, *TQV* and *3TNLV*, *TTLQV* and *3TLQV* only showed distinct peaks at 25, and did not provide any detailed information on other scales of interests (Fig. 2e).

Figs. 2f and 2g showed variance plots of the transect *i* which combined two single-scale transects with different fixed length cycles at 30 and 50, respectively. Fig. 2f showed similar results to Fig. 2d. *PQV*, *TQV*, *NLV* and *3TNLV* identified various phases at 7, 12, 23 and 38. *PQV* and *TQV* produced clear inflections and peaks which corresponded well with different phase

sizes; while *NLV* and *3TNLV* often showed clear structures on the first and second inflections but dampened the structures at larger scales. *TTLQV* showed a plateau with an obscure peak at 20, which represented the mean of two fixed length cycles (Fig. 2g). However, *3TLQV* displayed a clear peak at 35, corresponding to the larger fixed length cycle, and a less obvious shoulder at 15, corresponding to the smaller fixed length cycle.

Existing sample data

The plots of *TTLQV* and *3TLQV* for the sparrow transect (Fig. 3a) displayed peak values at block size 5 and 6 respectively. *NLV*, *PQV*, *3TNLV* and *TQV* exhibited their first peaks or inflections at block size 3. After reaching the first inflections, *PQV* and *TQV* displayed a plateau. The second inflection of the plateau can be observed at 7 or 10, but is unclear. Similarly, neither *NLV* nor *3TNLV* provided a clear second inflection. This could indicate that the pattern of the larger phase was not sharp or was randomly varied. Results from directly measuring the gap and patch size based on the threshold indicated that the mean patch size was 2.44 and mean gap size was 7.65 (App. 1). For the patch-gap analysis, the plot values peak at index W_k and Y_k , which can be interpreted as mean gap and patch sizes respectively, give the mean gap size at 11 and the mean patch size at 3 (App. 2: sparrow nests). Overall, the results from either quadrat-variance methods or patch-gap detection methods agreed well with each other by providing the mean patch size ca. 3 and gap size ca. 10.

The variance plots of *TTLQV*, *3TLQV* and *3TNLV* of the ant hills transect displayed a peak value at 4. *NLV* gave a peak value near 3. The first inflection of the plateau in *PQV* was near 4, and the second inflection at 6. Directly measuring the patch-gap size resulted in a mean gap size of 6.0 and a patch size of 3.14 (App. 1). The results from the patch-gap analysis indicated that the mean gap size was 7 and the mean patch size was 4 (App. 2: ant hills). Although the results from these two patch-gap measurements are slightly different, they approximately corresponded with the observations from the *PQV* analysis. Overall, the results indicated that mean gap size was ca. 6 and mean patch size was ca. 3.

Ludwig & Reynolds (1988) interpreted that the mean distance between patch centres will be twice the block distance corresponding to the peak values of *PQV* and *TTLQV*. While this was true for the *TTLQV*, for the *PQV* it was valid only if the patch size equalled the gap size. In most cases, including the above examples, the *PQV* did not display a distinct peak.

Discussion

When mean patch size equals mean gap size along a transect, *TTLQV*, *3TLQV*, *NLV*, *3TNLV*, *PQV* and *TQV* display distinct peaks, which represent the mean size of patches (or gaps). When patch and gap size are unequal, the variance plot of these quadrat variance methods behave differently. The variance plots of *TTLQV* still show a clear peak, which represents the mean size of patches and gaps but the peak often has a drift (Dale & Mah 1998). *3TLQV* corrects the peak drift problem of *TTLQV* and gives more accurate estimation of the mean size than *TTLQV* (Dale 1999). For *NLV*, the first peak represents the mean size of the smaller phases (gaps or patches). The shoulder of *NLV*, which is often neglected in previous research, reveals the mean size of larger phases. For *PQV*, the variance plot displays a flat-topped plateau, in which the first inflection represents the mean size of the smaller phase, either gaps or patches, and the second inflection represents the mean size of the larger phase. This interpretation of *PQV* is opposite to that provided by Carpenter & Chaney (1983). They believed that the first peak of *RPQV*, which is a close relative of *PQV*, represented the mean size of patches. However, in all their simulation data, except the equal-equal artificial transect, the mean gap sizes were always larger than patch sizes. For example, for the fixed-fixed simulated transect, they set the patch size as eight units and gap size as 43 units, while in fixed-random simulations, gap size was 43 ± 2 units and the patch size remained 8. Therefore, according to our study, the first inflection of *PQV* indicated the mean size of smaller phases, which represented the patch size in their study. That is why they claimed the first peak of *RPQV* represented the mean size of patches.

Our interpretation of *PQV* also contradicted Dale & Mah (1998). They believed that the peak value of *PQV* indicated the mean distance between the centre of a gap and the centre of a patch. Dale (1999) commented that a weakness of the *PQV* method was that it did not give a clear peak, but a flat-topped trapezoid. As shown in this study, only if the gap size is equal to the patch size does the *PQV* method give a sharp peak (Fig. 1c). However, the flat-topped plateaus provide the opportunity of understanding more fully the scale of pattern by revealing not only the mean size of gaps and but also the mean size of patches. In comparison, the *TTLQV* method only provides the mean distance between patches and gaps. Although the peak value of *NLV* clearly exhibited the size of the smaller phases, it dampens the second inflection (Fig. 1), which represents the size of the larger phases. The ability of *PQV* to differentiate the patch and gap sizes results from its being based on paired quadrats, while methods such as *TTLQV* are based on blocked

quadrats, which could confound the effect of gaps and patches (Ludwig & Goodall 1978). *NLV* essentially can be considered as the differences between adjacent *TTLQV* terms (Dale 1999).

The randomness effects on *TTLQV*, *NLV* and *PQV* also behaved differently across measures. In all our simulation and sample data, variance plots of *TTLQV* tended to exhibit a clear peak. The advantage of this characteristic is that *TTLQV* can easily reveal the scale of mean patch and gap size even when they vary randomly. On the other hand, it means that *TTLQV* provides no further information about the structure of patches and gaps (e.g. are patch sizes relatively constant or distributed randomly?). With *NLV* or *PQV*, the variance plot gave a clear peak or inflection if the corresponding phase was relatively constant. For example, both *NLV* and *PQV* gave the distinct first peaks at 4, but the second inflections at 10 were less clear (Fig. 1d). This corresponded well with the fact that the smaller phase of transects d has the fixed size at 4, and the larger phase has the size randomly varying from 1 to 20 with the mean ca. 10. Conversely, *NLV* and *PQV* showed the round shapes of the first peak and inflection, while exhibiting a sharp change at the second inflection (Fig. 1e). This is because the smaller phases of transect e varied randomly from 1 to 20, and the larger phases had a fixed size at 35. Therefore, examining the shape of *PQV* and *NLV* can provide information about not only the scale of the patch and gap size, but also their spatial structure.

It is commonly believed that three-term quadrat variance methods are more robust in dealing with trend data (Dale 1999). As shown in Fig. 2b, c, *3TLQV*, *TQV* and *3TNLV* were not sensitive to the simulated trend data. However, their two-term counterparts (*TTLQV*, *PQV* and *NLV*) showed increasing variance in the presence of trend data. In particular, *TTLQV* increased dramatically after the first 20 block sizes (Fig. 2c) and was very susceptible to the trend data. In all simulated data, *3TLQV* outperformed *TTLQV*. *3TLQV* was able to overcome the peak drift problem of *TTLQV*. However, *3TNLV* and *TQV* did not consistently outperform their two-term counterparts (*NLV* and *PQV*). Although *3TNLV* and *TQV* were able to detect not only the mean distance between gaps and patches (e.g. Fig. 1a and b) but also the sizes of patches and gaps (e.g. Fig. 1d, e), these advantages came at a cost. The features identified by *3TNLV* and *TQV* could dampen each other, and make interpretation difficult. For example, Fig. 1a showed the results of quadrat variance analysis of transect a. *3TNLV* displayed a distinct peak at 6, which is the mean distance between gaps and patches. However, it not only dampened the first inflection at 4 (representing the size of the smaller phase) but also made the characteristics of

the size of larger phase unobservable. Another example, 3TNLV exhibited the peak value at 5 (representing the size of the smaller phase) for transect b (Fig. 1b), and dampened the shoulder at 6 (representing the mean distance between patches and gaps). Therefore, the advantages of 3TNLV and TQV to detect not only mean distance between patches and gaps but also the size of gaps and patches could confuse the interpretation of the scale when the pattern of the transect is unknown.

In conclusion, we suggest that in the absence of trend data, combinations of PQV, 3TLQV, NLV and gap-patch measurements should be used to provide supplementary and comprehensive spatial information about transect data. However, when trend data are encountered, combining two-term and three-term quadrat variance methods could provide a better understanding of the true pattern of transect data.

Acknowledgements. We thank Dr. Jan Lepš and three anonymous reviewers for their helpful comments on the manuscript.

References

- Akashi, N. 1996. The spatial pattern and canopy-understorey association of trees in a cool temperate, mixed forest in western Japan. *Ecol. Res.* 11: 311-319.
- Bailey, T.C. & Gatrell, A.C. 1995. *Interactive spatial data analysis*. Harlow, Essex, UK.
- Carpenter, S.R. & Chaney, J.E. 1983. Scale of spatial pattern: Four methods compared. *Vegetatio* 53: 150-160.
- Carter, A.J. & O'Connor, T.G. 1991. A two-phase mosaic in a savanna grassland. *J. Veg. Sci.* 2: 231-236.
- Cowling, A. 1998. Spatial methods for line transect surveys. *Biometrics* 54: 828-839.
- Dai, X. & van der Maarel, E. 1997. Transect-based patch size frequency analysis. *J. Veg. Sci.* 8: 865-872.
- Dale, M.R.T. 1999. *Spatial pattern analysis in plant ecology*. Cambridge University Press, Cambridge, UK.
- Dale, M.R.T. & MacIsaac, D.A. 1989. New methods for the analysis of spatial pattern in vegetation. *J. Ecol.* 77: 78-91.
- Dale, M.R.T. & Mah, M. 1998. The use of wavelets for spatial pattern analysis in ecology. *J. Veg. Sci.* 9: 805-814.
- Dale, M.R.T., Dixon, P., Fortin, M.-J., Legendre, P., Myers, D.E. & Rosenberg, M.S. 2002. Conceptual and mathematical relationships among methods for spatial analysis. *Ecography* 25: 558-577.
- Edwards, G.R., Parsons, A.J., Newman, J.A. & Wright, I.A. 1996. The spatial pattern of vegetation in cut and grazed grass white clover pastures. *Grass For. Sci.* 51: 219-231.
- Galiano, E.F., Castro, I. & Sterling, A. 1987. A test for spatial pattern in vegetation using a Monte-Carlo simulation. *J. Ecol.* 75: 915-924.
- Hill, M.O. 1973. The intensity of spatial pattern in plant communities. *J. Ecol.* 61: 225-235.
- Lepš, J. 1990. Comparison of transect methods for the analysis of spatial pattern. In: Krahulec, F., Agnew, A.D.Q., Agnew, S. & Willems, J.H. (eds.) *Spatial processes in plant communities*, pp. 71-82. Academia Press, Prague, CZ.
- Ludwig, J.A. & Goodall, D.W. 1978. A comparison of paired-with blocked-quadrat variance methods for the analysis of spatial pattern. *Vegetatio* 38: 49-59.
- Ludwig, J.A. & Reynolds, J.F. 1988. *Statistical ecology: A primer of methods and computing*. Wiley, New York, NY, US.
- Ma, K.M., Zu, Y.G. & Godron, M. 2001. Scale correlation between vegetation and soil in larch forest, NE China. *J. Environ. Sci. China* 13: 51-57.
- Perry, J.N., Liebhold, A.M., Rosenberg, M.S., Dungan, J., Miriti, M., Jakomulska, A. & Citron-Pousty, S. 2002. Illustrations and guidelines for selecting statistical methods for quantifying spatial pattern in ecological data. *Ecography* 25: 578-600.
- Ribeiro, K.T. & Fernandes, G.W. 2000. Patterns of abundance of a narrow endemic species in a tropical and infertile montane habitat. *Plant Ecol.* 147: 205-218.
- Ripley, B.D. 1976. The second-order analysis of stationary point processes. *J. Appl. Probab.* 13: 255-266.
- Schaefer, J.M. 1993. Spatial patterns in taiga plant communities following fire. *Can. J. Bot.* 71: 1568-1573.
- Schaefer, J.A. & Messier, F. 1994. A paired-quadrat method for use in multiscale ordination. *Vegetatio* 113: 9-11.
- Usher, M.B. 1983. Pattern in the simple moss-turf communities of the sub-Antarctic and maritime Antarctic. *J. Ecol.* 71: 945-958.
- Verhoef, J.M., Cressie, N.A.C. & Glenn-Lewin, D.C. 1993. Spatial models for spatial statistics – some unification. *J. Veg. Sci.* 4: 441-452.
- Wilson, C. & Gurevitch, J. 1995. Plant size and spatial pattern in a natural population of *Myosotis micrantha*. *J. Veg. Sci.* 6: 847-852.
- Yang, X.B., Snow, J.P. & Berggren, G.T. 1991. Patterns of rhizoctonia foliar blight on soybean and effect of aggregation on disease development. *Phytopathology* 81: 287-293.

Received 9 October 2003;

Accepted 7 August 2004.

Co-ordinating Editor: J. Lepš.