

Spatial point pattern analysis of available and exploited resources

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Lancaster, J. and Downes, B. J. 2004. Spatial point pattern analysis of available and exploited resources. – *Ecography* 27: 94–102.

A patchy spatial distribution of resources underpins many models of population regulation and species coexistence, so ecologists require methods to analyse spatially-explicit data of resource distribution and use. We describe a method for analysing maps of resources and testing hypotheses about species' distributions and selectivity. The method uses point pattern analysis based on the L-function, the linearised form of Ripley's K-function. Monte Carlo permutations are used for statistical tests. We estimate the difference between observed and expected values of $L(t)$, an approach with several advantages: 1) The results are easy to interpret ecologically. 2) It obviates the need for edge correction, which has largely precluded the use of L-functions where plot boundaries are "real". Including edge corrections may lead to erroneous conclusions if the underlying assumptions are invalid. 3) The null expectation can take many forms, we illustrate two models: complete spatial randomness (to describe the spatial pattern of resources in the landscape) and the underlying pattern of resource patches in the landscape (akin to a neutral landscape approach). The second null is particularly useful to test whether spatial patterns of exploited resource points simply reflect the spatial patterns of all resource points. We tested this method using over 100 simulated point patterns encompassing a range of patterns that might occur in ecological systems, and some very extreme patterns. The approach is generally robust, but Type II decision errors might arise where spatial patterns are weak and when trying to detect a clumped pattern of exploited points against a clumped pattern of all points. An empirical example of an intertidal lichen growing on barnacle shells illustrates how this technique might be used to test hypotheses about dispersal mechanisms. This approach can increase the value of survey data, by permitting quantification of natural resource patch distribution in the landscape as well as patterns of resource use by species.

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In nature, resources are often patchily distributed and such patchiness can affect both population numbers and the coexistence of species (Chesson 2000). Spatially, resources may be described as patches within a landscape: patches can be large and form mosaic landscapes, or small and scattered through the study area. Patterns generated by this second kind are of particular interest here: resource patches that can be described as discrete "points" in the landscape. Ecological examples are abundant and include emergent rocks in rivers used as oviposition sites by aquatic insects (Peckarsky et al.

2000, Reich and Downes 2003), parasites and their hosts (Tenhumberg et al. 2001, Tripet et al. 2002), food plants for specialist herbivores (Fahrig and Paloheimo 1988, Doak 2000), fruit or fungi for flies with larvae that consume those resources (Atkinson and Shorrocks 1984, Krijger and Sevenster 2001) and carrion fly communities (Ives 1991).

Describing the spatial distribution of resources is challenging, given that resource "points" may be clumped or over-dispersed at multiple spatial scales. A further challenge is to describe how organisms use those

Accepted 29 July 2003

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ISSN 0906-7590

spatially distributed resources and, ultimately, to understand the consequences of resource distribution patterns for population-level processes. In all these examples, mobile animals select and exploit resource points from an array of possible resource points, and some points are not exploited. The distribution of resources is often driven by environmental factors (e.g., geomorphic processes in rivers distribute boulders that may become oviposition sites), but the selection of resource points by organisms, coupled with differential survival following selection, may produce different patterns. Understanding the interactions between these two processes, i.e., how different organisms interact with variable landscapes, is integral to understanding population dynamics.

To begin to de-couple effects of different resource arrays in a landscape from the effects of selection behaviour and differential survival of species on those resources, it is important to examine exploited resource points within the context of all available resource points. Surprisingly little attention, however, has been directed at comparing the spatial patterns of available and exploited points. Numerical techniques exist for some related aspects of population dynamics on patchy resources, such as the aggregation model of coexistence (Hartley and Shorrocks 2002), but these models are rarely spatially-explicit (i.e., directly consider the arrangement of resource patches in space) and this may be important in some situations (Heard 1998, Remer and Heard 1998). There are many spatially-explicit studies of organism-landscape interactions that view landscapes as a mosaic of habitat types, and they use different numerical techniques, appropriate to that scenario (e.g. With and Crist 1995, McIntyre and Wiens 2000, Palmer et al. 2000). Such studies are often concerned with ecosystem-level issues like habitat fragmentation and connectivity, and less with how resource patch distribution might mediate coexistence or regulate populations (but see Silver et al. 2000). Thus there is a need for methods to de-couple the pattern of resource patch exploitation from the background of available patches and, eventually, these processes need to be integrated into tests of population processes.

How does the spatial distribution of exploited resources compare with the distribution of all resources, and what ecological processes generate the observed patterns? Are exploited resources regularly spaced, perhaps through inter-individual repulsion, despite an underlying clumped pattern of all resources? In this paper, we present a method for tackling these questions. This method uses spatially explicit, point pattern analysis coupled with tests of "null" models generated by posing ideas about how organisms are using resource patches (akin to neutral landscape models: With and King 1997). The method allows relatively sophisticated information to be drawn from basic survey data, with

these results then enabling the design of experimental tests of hypotheses.

Background and the problem of edge correction

Analysis of spatial point patterns commonly involves Ripley's K-function (Ripley 1976, 1981) and the related functions of second-order neighbourhood analysis. Various forms of such spatial pattern analysis are widely used in many disciplines (e.g., epidemiology, geomorphology, criminology) and are becoming more common in ecological studies, especially in plant ecology. The simplest application is to use the mapped position of points (e.g., plants), expressed as x:y co-ordinates, in a univariate analysis to describe spatial pattern as clumped, random or over-dispersed (Ward et al. 1996, Cole and Syms 1999). Extensions of this K-based point pattern analysis allow examination of spatial association in two-species interactions (Andersen 1992), such as competition (Martens et al. 1997) and facilitation (Haase 2001), and could be extended further to examine processes involving more than two species or categories of points (Lotwick and Silverman 1983, Penttinen et al. 1992). Another logical extension involves comparing the pattern of "marked" points (e.g., exploited resource points) to the pattern of all points (Besag and Diggle 1977, Diggle 1983, Rowlingson and Diggle 1993), but this has received relatively little attention from ecologists (but see Penttinen et al. 1992). Andersen (1992) explored this idea a little, but concluded that his K-function plots were not "conceptually transparent" and hence difficult to interpret ecologically. Our objective was to develop a robust and easily interpreted technique that calculates the difference between two spatial patterns (marked vs all points) and tests whether the pattern of marked points is significantly different from the underlying pattern of all points.

Because plots of resource points necessarily have boundaries (real in some habitats and artificially imposed in others), edge correction is an important issue associated with K-function analyses in ecological studies and it may restrict the range of situations in which these methods can be used. Edge corrections consider points near the plot boundary, where the real number of neighbouring points may be underestimated if some points lie outside the plot. Thus an edge correction is applied in which points near the boundary are weighted more heavily than those closer to the centre. Hitherto, virtually all ecological applications of K-functions have included edge correction and Goreaud and Pélissier (1999) recommend the use of edge correction for ecological interpretations, but this view is not unanimous (Ward and Ferrandino 1999). The suitability of edge correction depends on the underlying assumption that the region surrounding the study plot has a point

density and distribution pattern similar to areas within the plot. For many ecological situations, this assumption may be inappropriate and edge correction difficult to justify. Many habitats have hard, "real" edges, e.g., aquatic-terrestrial boundaries, and the point pattern cannot possibly extend beyond the plot boundary. It may not be feasible (or ecologically sensible) to map only the interior of a habitat patch in order to satisfy this assumption, especially where overall point density is low. Indeed, points near the edge of the plot may contribute little to the overall ecological processes and, thus, weighting these points may be erroneous. If edge correction is not justified ecologically, then we need to explore alternative methods of point pattern analysis for these situations. K-based methods without edge correction are poorly developed, but we do know that applying edge correction when it is unwarranted may lead to erroneous conclusions (Baddeley et al. 2000). Gignoux et al. (1999) found that the power of statistical tests was increased without edge correction, especially if the number of points is small (<20) and the pattern is clumped. Nevertheless, using a statistical argument for omitting edge correction may be difficult to justify if it is inconsistent with the ecological context. We explore ways in which K-based analyses can be used to describe point patterns when edge correction is inappropriate, and we assess the effect of edge correction when comparing the patterns of marked vs all points. Techniques with widespread applicability are clearly advantageous.

Method

Neighbourhood analysis of point patterns is based on distances between all pairs of points; it counts the number of points within a certain distance, t , of each point, with t taking a range of values. Ripley's K-function describes the cumulative frequency distribution of all point-to-point distances:

$$K(t) = n^{-2} A \sum_i^n \sum_{j \neq i}^n w_{ij} I_t(u_{ij})$$

where: t is the radius of a circle centred on a point in the pattern, n is the total number of points, A is the plot area, w_{ij} is a weighting factor to correct for edge effects, and I_t is a counter variable which is set to 1 if the distance u_{ij} between points i and j is $\leq t$, otherwise $I_t = 0$. Commonly, $K(t)$ is presented as the linearised L-function (Besag 1977):

$$L(t) = \sqrt{K(t)/\pi} - t$$

This is often easier to interpret than $K(t)$ as, under complete spatial randomness, $L(t) = 0$ for all t . If points are clumped in space, $L(t) > 0$; if points are regularly

dispersed, $L(t) < 0$. The significance of any observed patterns are usually assessed by comparing the observed distribution function with that expected under complete spatial randomness (CSR). In other words, we ask whether the observed spatial pattern of n points is more clumped or more evenly distributed than a random arrangement of n points in the plot. The 95% confidence envelope for CSR is obtained by Monte Carlo permutations.

There are several different methods of calculating a weighting factor to correct for edge effects (e.g., see review by Haase 1995). Perhaps the most widely used is Ripley's local weighting factor, in which w_{ij} is computed as the inverse of the proportion of the circumference of the circle (centred on i , passing through j and with radius u_{ij}) which is inside the study area. We used formulae for local weighting factors published in Goreaud and Pélissier (1999) for rectangular study areas, including long narrow plots, i.e., edge correction includes cases where the circle intersects with three sides of the study plot. This allows computation of $L(t)$ for t up to half of the longest side of a rectangular plot, instead of the more usual limit of t at half the shortest side of a rectangle (Diggle 1983), as set by the computations for local weighting factors.

Simulated point patterns were run for over 100 different combinations and permutations of square or rectangular plots, of random, clumped or even distributions, of all and marked points. These simulated landscapes are hypothetical and hence artificial, but our aim was to include a very wide range of spatial patterns that might occur in ecological systems and to test the limits of our methods with some very extreme patterns. All plots had the same area and had 200 points, of which 50 were marked as "exploited". All Monte Carlo tests used 999 permutations. Programs were written on a Macintosh computer using REALbasic (ver. 3.0, 2001).

Comparing distribution functions

We illustrate our results with two extreme examples. Firstly, Fig. 1a illustrates a square plot in which all points are weakly clumped, but marked points are randomly arranged in space (despite the clumped background) and are a random selection of the points available. [Note that a random sample of points from a clumped pattern will usually be clumped in space also. Some random samples, however, will be randomly or evenly distributed in space. The probability of such an event occurring depends on the underlying pattern strength and the number of points. This could arise in some ecological applications so this extreme case warrants consideration.] Secondly, Fig. 1b illustrates a rectangular plot in which all points are arranged into five clusters, marked points are randomly distributed in

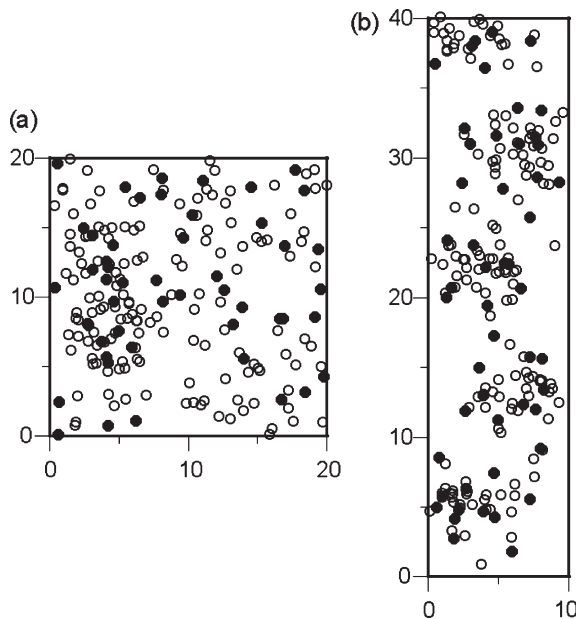


Fig. 1. Maps of two simulated point patterns used for illustration. Fifty of the 200 points are marked and marked points are indicated by filled symbols. Both plots have the same area; distance units are arbitrary. (a) Square plot where all points are weakly clumped; marked points are randomly distributed in space and relative to the underlying pattern. Twenty-five percent of all the points are clumped in 15% of the area. (b) Rectangular plot where all points are arranged in five clumps with $\sim 20\%$ of all points in each clump; each clump covers $\sim 16\%$ of the total area. Marked points are randomly distributed in space, but evenly distributed relative to the underlying pattern.

space, and thus more evenly distributed than the underlying clumped pattern. We can illustrate these patterns by examining the L-functions. For the square plot, the L-function for all points (calculated with edge correction), lies above the confidence envelope for CSR and clearly indicates clumping (Fig. 2a). For the rectangular plot, the L-function for all points (calculated with edge correction), lies above the confidence envelope for CSR at ~ 3 units, indicating clumping within clusters (Fig. 3a). Significant clumping is also apparent at ~ 11 and 19 units. This “ripple effect” reflects peaks in point-to-point distances between clusters and is typical of patterns with multiple clumps close together.

If edge correction is excluded from the analysis and the term w_{ij} is removed from the calculation of $K(t)$, (e.g., the underlying assumptions are violated so that an edge correction is inappropriate, as discussed above), then simple examination of the L-function and the confidence envelope under CSR may be inadequate to define the spatial pattern. An L-function that excludes edge correction typically becomes increasingly negative after just a few t and the resultant graphs are difficult to interpret, because values for the observed and expected $L(t)$ converge and become indistinguishable relative to the scale of the y-axis (Fig. 2b and 3b). With edge

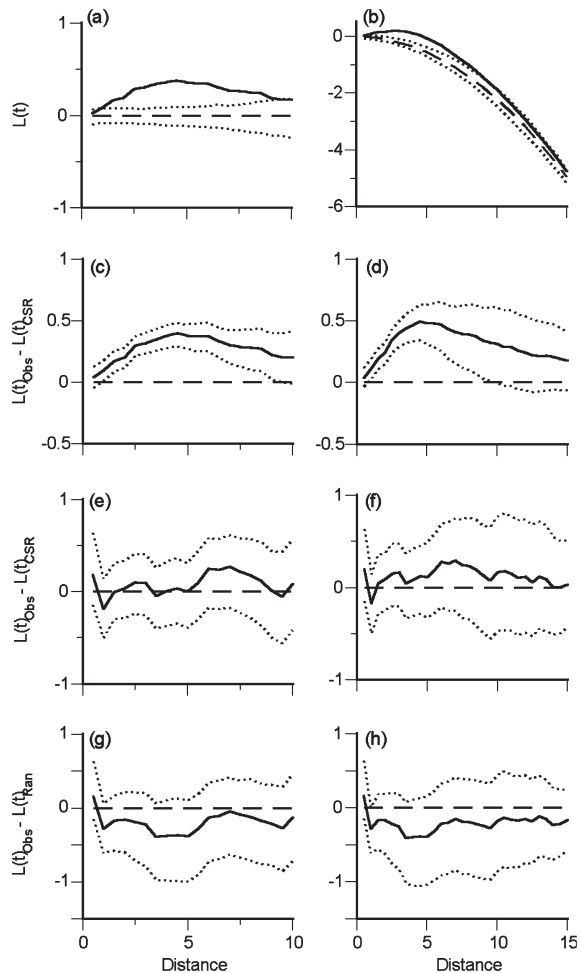


Fig. 2. Point pattern analyses of square plot illustrated in Fig. 1a. Edge correction was included for all analyses in the left column and excluded from those on the right. (a) and (b) spatial pattern of all points, as indicated by the L-function. Solid line indicates observed L-function of all points, dashed line indicates L-function under CSR, dotted lines indicate a 95% confidence envelope for CSR. (c) and (d) spatial pattern, indicated by the mean difference between the observed L-function and the L-function under CSR, of all points, and (e) and (f) of marked points. Solid line indicates the mean difference between L-functions, dotted lines indicate 95% confidence envelope for the difference, dashed line indicates the null hypothesis of no difference. (g) and (h) spatial pattern of marked points compared with underlying distribution of all points. Solid line indicates the mean difference between the observed L-function of marked points and the L-function of a random selection of all available points, dotted and dashed lines as in c–h.

correction, CSR is indicated by $L(t) = 0$ for all t ; without edge correction, the L-function under CSR is more complex. An alternative approach is required.

A way forward is to consider that the value of $L(t)$ may be of little interest. Of greater interest and perhaps of more utility in describing spatial pattern is the position of the observed L-function in relation to the confidence envelope, i.e., the difference between the

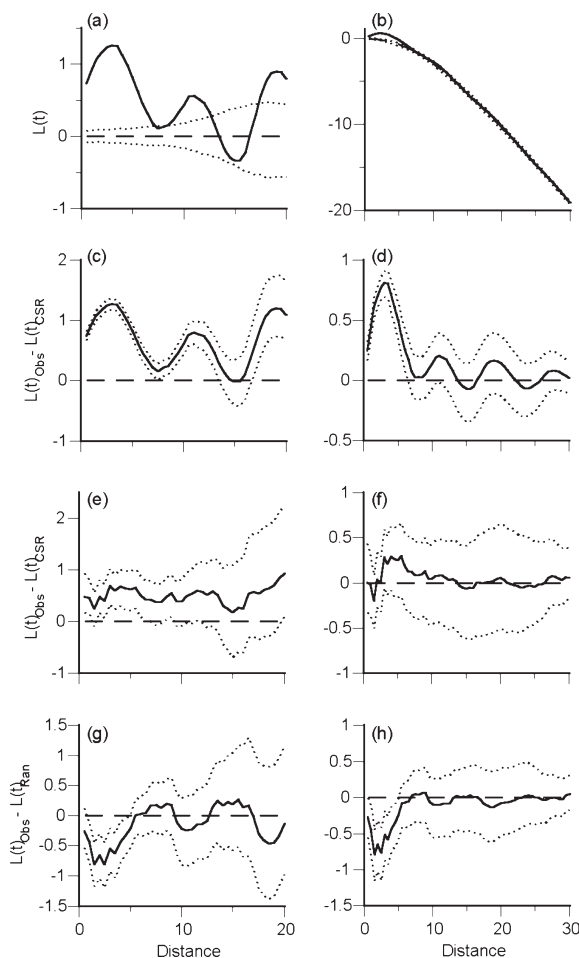


Fig. 3. Point pattern analyses of rectangular plot illustrated in Fig. 1b. See Fig. 2 legend for explanation.

observed L-function and the L-function under CSR, $L(t)_{\text{Obs}} - L(t)_{\text{CSR}}$. The null hypothesis is that there is no difference between the two functions, i.e., $L(t)_{\text{Obs}} - L(t)_{\text{CSR}} = 0$ for all t . To interpret the spatial pattern statistically, Monte Carlo permutations are used to calculate the mean difference and the confidence envelope about the difference. If the observed difference between L-functions is positive (i.e., the mean difference and its confidence envelope lie above the null hypothesis of no difference), then the points are more clumped than expected by chance. If the observed difference between L-functions is negative, then the points are evenly spaced. If the null hypothesis lies within the confidence envelope, this indicates a random spatial pattern. This method of calculating the difference between L-functions should be equally appropriate for analyses with or without edge correction. Similarly, Baddeley et al. (2000) describe a method for estimating the J-function of spatial point patterns in which any edge effect bias in the test statistic is accounted for by similar biases in the null distribution of the test statistic.

Using the above approach in all our simulations, the inclusion or exclusion of edge correction had either no effect on the interpretation of spatial pattern (i.e., clumped, random or even), or differences in interpretation could be related directly to the assumptions underlying edge correction. For the clumped pattern in Fig. 1a, the mean difference between L-functions and its confidence envelope is positive and indicates clumping, in analyses with and without edge correction (Fig. 2c, d). Similarly, the difference between L-functions is positive in Fig. 3c, d and indicates a clumped spatial pattern. Only Fig. 3c indicates significant clumping at several scales (as in Fig. 3a), and whether this interpretation is correct depends entirely on the ecological context and the assumptions underlying edge correction. If the point pattern does indeed extend in all directions beyond the plot boundary, then edge correction would be appropriate and we could expect statistically significant “ripples” that suggest clumping at multiple scales (Fig. 3c). If the pattern does not extend beyond the plot boundary, then visual examination of Fig. 1b suggests that clumping should be significant at only the smallest scale, as shown in Fig. 3d. The J-function estimates of Baddeley et al. (2000) also suggest that calculations with and without edge correction may provide contradictory conclusions. Note that in our simulations (most of which are not reported here owing to space constraints), square plots were less sensitive than elongated plots to the inclusion/exclusion of edge correction. Regardless of plot shape, the most sensitive patterns involved a few large clumps (especially if clumping was weak, as in Fig. 1b). Overall, the method of examining the difference between L-functions appears to be robust, but the decision of whether to include edge correction must be considered carefully and with reference to the ecological context of the study.

Using a neutral landscape approach

If the study objectives focus on the spatial pattern of n' marked (i.e., exploited) points rather than the pattern of all points, then several different neutral landscape models, rather than just complete spatial randomness, could be employed. The method, however, of assessing point patterns by calculating the difference between two L-functions remains virtually identical for any neutral landscape model. We illustrate this by exploring two neutral landscapes. Firstly, we compared the L-function of n' marked points with the L-function of n' points under CSR. Ecologically, this examines the spatial pattern of marked points, regardless of the underlying pattern of all available points. Analyses followed the same procedures as outlined above for analysing the spatial pattern of all points. Secondly, we tested whether the distribution of marked points differed from the

spatial pattern of all available points, following a suggestion of Rowlingson and Diggle (1993). Ecologically, this tests whether the pattern of marked points can be explained by random selection (by insects seeking oviposition sites, for example) given the underlying pattern of all points, which provides the null expectation. For this analysis, a random sample of n' points (where n' is the same as the number of marked points) is selected from the n available points. The null hypothesis, that marked points are a random selection of those available, is reflected by no difference between the two L-functions, i.e., $L(t)_{\text{Obs}} - L(t)_{\text{Ran}} = 0$ for all t . As above, Monte Carlo permutations are used to calculate the mean difference and a 95% confidence envelope around the difference. The position of the mean difference and its confidence envelope relative to the null hypothesis of no difference is again used to determine whether marked points were clumped, random or evenly distributed relative to the underlying spatial pattern.

The choice of neutral landscape may influence the perception and interpretation of whatever process is involved in generating the marked points. Careful consideration of the ecological context and a clear description of the hypothesis under test is required when selecting the neutral landscape as it determines the null expectation. When we ask questions about the distribution of marked points irrespective of the underlying distribution (neutral landscape one, above), we cannot distinguish between different types of explanations that might produce similar patterns. A finding that marked points are clumped might be explained by selective behaviour of organisms that produces that pattern, but clumping can also be caused by random selection by organisms moving over a landscape of clumped patches. It is the second type of neutral landscape that allows us to test whether spatial patterns of marked points are more or less than what would be expected, given the underlying distribution of resource patches. We suggest that, in many cases, the latter tests may be more interesting and informative, given that we can start to rule out some explanations of patterns.

Further, the use of edge correction influenced the interpretation of spatial patterns for the first neutral landscape of CSR in some cases, but did not affect the second, that of the underlying pattern of all points. For the plot in Fig. 1a, edge correction had no impact on the interpretation, marked points are clearly arranged at random in space (Fig. 2e, f) and are a random selection of those available (Fig. 2g, h). The confidence envelope around the mean encompasses the null hypothesis of no difference in these four cases. It is perhaps paradoxical that a random selection of points from a clumped point pattern should result in a random pattern of marked points compared to CSR. This is because the marked points are low in number and a small proportion of the total (25%), and the underlying clumped pattern is weak

(25% of all points in 15% of the area). If these were real data from an ecological system, the challenge would be to determine whether the limits of statistical power precluded detecting a significant pattern, and how strong patterns need to be before they become ecologically meaningful. Such methods of power analysis and effect size have yet to be developed for this method. For the plot in Fig. 1b in which the point pattern is stronger, if the neutral landscape is CSR, the difference between L-functions was positive in the analysis with edge correction, suggesting a clumped spatial pattern at ~ 3 units (Fig. 3e). In contrast, the L-functions did not differ significantly in the analysis without edge correction, suggesting a pattern that is not significantly different from CSR (and no evidence of selection by organisms) (Fig. 3f). Thus, the ecological validity of assumptions underlying the use of edge corrections are crucial to the interpretation. For the second neutral landscape (i.e., to determine whether the spatial pattern of marked points is independent of the underlying pattern) then analyses with and without edge correction both indicated an even distribution over small distances (Fig. 3g, h). We would have some suggestive evidence that there is selection by organisms that is not explained by the underlying distribution of patches.

This test of whether the spatial pattern of marked points is independent of the underlying point pattern appears to be robust and performed satisfactorily in all our simulations, although only two are presented here. This is encouraging as it means this technique can be applied to address ecological questions in a wide range of situations and habitats, including those where sample plots are irregular shapes (hence making edge corrections computationally difficult) and where the assumptions underlying edge correction are invalid. Additionally, the distance scale (i.e., maximum t) need not be limited (by computational constraints) to half the longest side of a rectangular plot if no edge correction is used, and this increases the scope for detecting features of the pattern that are large-scale relative to the plot size. Perhaps the most "problematic" of our simulations involved weak spatial patterns and a relatively small number of marked points (as in Fig. 1a and discussed above) and simulations involving clumped distributions of both all and marked points. To detect a clumped distribution of marked points, over and above any underlying clumping, required very strong clumping of marked points. For example, strong clumping might entail $> 50\%$ of marked points in a single cluster against a background of 25% of all points in a single cluster. This difficulty remained regardless of whether the clump of marked points coincided with the background clump of points. The risk of a Type II error may be high when dealing with ecological data with these characteristics. Some assessment of the power or sensitivity of the test to detect different degrees of clumping might be beneficial

in those situations. Alternatively, clump recognition techniques may prove more useful (Coomes et al. 1999), depending on the study objectives.

Empirical example

We illustrate the method of comparing available and exploited resource patches (without edge correction) using an example of an intertidal lichen, *Pyrenocollema halodytes* (Nyl.) R.C. Harris (1987), that grows endolithically on barnacle shells. In this example, barnacles are potential resource patches that can be mapped as a point pattern; barnacles with lichen are exploited patches (marked points). Direct observation of dispersal or colonisation of lichens is rare and most studies rely on indirect methods (Warren 2003). Point pattern analysis may be useful to test hypotheses about modes of dispersal in some situations. At our study site in SE Scotland (56°01'N, 2°35'W), the intertidal zone was very gently sloped and comprised of isolated, angular cobbles and boulders of basalt, in a matrix of gravel, silt and seaweed. *Pyrenocollema halodytes* was common and occurred almost exclusively on barnacles, *Semibalanus balanoides* (Linnaeus), attached to the upper surfaces of these large rocks. Some barnacles did occur in the matrix between large rocks, but at a much lower density and these rarely hosted the lichen. Thus, rocks are hard-edged patches with barnacles and lichens, and we cannot assume that the pattern extends beyond the rock boundary. Dispersal of lichens is complex and, at this small, within-rock scale, *P. halodytes* could colonise barnacles through vegetative spread of a single thallus onto adjacent barnacles, or via current-assisted dispersal of various propagules (Bailey 1976). If vegetative spread is the dominant form of colonisation, we might expect the spatial pattern of barnacles with *P. halodytes* to be more clumped than the underlying pattern of barnacles. Alternatively, propagules are likely to be deposited at random over the rock surface and barnacles with *P. halodytes* are likely to reflect the underlying pattern of barnacles if this is the major form of colonisation.

The spatial pattern of barnacles with and without lichen were mapped on the upper, flat surface of individual rocks, small enough to transport to the laboratory. Each barnacle was examined under a microscope at 40 \times and those with *P. halodytes* were marked with a water soluble, non-toxic ink. The rock surface was then photographed and x:y co-ordinates of each barnacle and the rock boundary were determined using the public domain software NIH IMAGE program (developed at the US National Institutes of Health and available on the Internet at <<http://rsb.info.nih.gov/nih-image>>). The results of one such mapping exercise are presented (Fig. 4a) for a rock of 162 cm² with 227 barnacles, 97 of which supported the lichen. Few

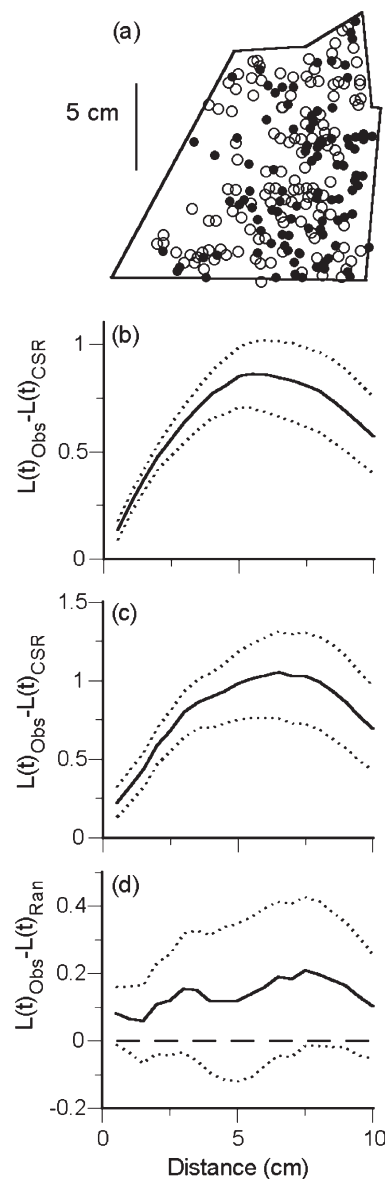


Fig. 4. (a) Map of barnacles and lichen on a rock. Open circles indicate barnacles without lichen; closed circles indicate barnacles with lichen. Point pattern analysis without edge correction of (b) all barnacles and (c) barnacles with lichen. Solid line indicates mean difference between the observed L-function and the L-function under CSR, dotted lines indicate 95% confidence envelope for this difference, dashed line indicates null hypothesis of no difference. (d) Spatial pattern of barnacles with lichens compared with the underlying distribution of all barnacles. Lines as in (b) and (c) except that we calculated the difference between the observed L-function and the L-function of a random selection of barnacles.

barnacles had settled on this rock recently and all were large enough to support *P. halodytes* (small, young barnacles rarely host lichens).

The spatial distribution of lichens appeared to reflect the underlying distribution of its resource patches, i.e.

barnacles, at this small scale. Barnacles were significantly clumped (Fig. 4b) and the gregarious nature of many intertidal barnacles is well known. Reproduction by sessile adults requires finding a mate in close proximity, and clumps are formed through the behaviour of settling larvae and interspecific interactions (Hartnoll and Hawkins 1985, Hills and Thomason 1996, Jeffery 2000). The pattern of barnacles with *P. halodytes* was also clumped (Fig. 4c) but, when compared with the underlying pattern, *P. halodytes* appeared to occur on a random selection of the available barnacles (Fig. 4d). This suggests that dispersal via propagules is the dominant form of colonisation at this scale. Spreading of a single thallus over several barnacles was observed in a few cases, but the occurrence of lichens on lone barnacles (Fig. 4a) or lichens restricted to the central, opercular plates and not covering the outer wall plates, is consistent with the idea of dispersal and colonisation by propagules.

Conclusion

This paper illustrates a technique based on the L-function (a form of Ripley's K-function (Ripley 1976, 1981, Besag 1977) for testing whether the spatial pattern of marked points is independent of the underlying pattern of all points. Importantly, edge correction is not required for this analysis. Edge correction has no impact on the interpretations and thus the technique has widespread applicability to a range of ecological situations. The general approach of calculating and plotting the difference between observed and expected L-functions can be used for any neutral landscape model that is suitable for Monte Carlo tests. More complex models, for example, might incorporate information on the quality of resource patches and the probability of individuals selecting certain kinds of patch (Lancaster et al. 2003). Neutral landscape models can take many forms and selecting the correct null model is crucial to making the correct ecological interpretation (With and King 1997). For example, marked points may be over-dispersed relative to the underlying clumped pattern of all points, yet appear to be randomly distributed when the neutral landscape is CSR (Fig. 3e vs 3g and 3f vs 3h). In the first case, we might hypothesise that some form of avoidance behaviour prevents individuals exploiting adjacent resource points.

As an added advantage, estimating the difference between observed and expected L-functions provides a means of examining spatial pattern when edge correction is inappropriate (Lancaster et al. 2003). It is often assumed (or even recommended) that edge correction is required for K- and L-function use in ecological contexts. Thus, either, K-based tests cannot be used in situations where the assumptions underlying edge cor-

rection are invalid, or, researchers may be tempted to include edge correction in order to do the analysis, even though assumptions may be invalid. The former need not be the case as, by emphasising the difference between L-functions rather than the actual value of L, analyses without edge correction are easily interpreted. The later scenario is more worrying as our simulations indicate that the inclusion/exclusion of edge effects can lead to different interpretations of spatial pattern (e.g., Fig. 3e, f) (see also Baddeley et al. 2000). The ecological context should be of prime importance for decisions regarding edge correction.

Our approach might be particularly valuable where experiments are required to test hypotheses about how patch distribution (density, dispersion, etc.) affects population numbers or species coexistence. As long as surveys of resource patch use are spatially-explicit, our approach provides both a quantification of resource patch distribution in the landscape, as well as a preliminary test of whether there is evidence of selectivity by organisms (Lancaster et al. 2003). This can better inform experimental tests, both in establishing a realistic layout of resources within experimental plots (e.g., degree of spatial aggregation of patches) as well as providing predictions of outcomes under different scenarios.

Acknowledgements – Thanks to Paul Reich and Rob Hale for their help collecting the data that motivated much of this. Thanks to Gareth Hughes for discussion of spatial statistics in the very early stages and to Lisa Belyea for the lichen. Financial assistance was provided by a British Ecological Society Small Ecological Project Grant and a Univ. of Melbourne International Collaborative Research Grant.

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