

# A positive relationship between local abundance and regional occupancy is almost inevitable (but not all positive relationships are the same)

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## Summary

1. Recent attempts to examine the role of different mechanisms in generating a positive abundance–occupancy relationship failed to properly distinguish between Brown's (1984) sampling artefact, and the form of relationship to be expected from a random distribution of individuals.
2. Because random distributions generate a positive relationship, one can never predict that removing the influence of some or all of the mechanisms will lead to 'no relationship'.
3. In considering how the spatial aggregation of individuals might influence the form of the abundance–occupancy relationship it is demonstrated that curvilinear and triangular relationships are expected, and that correlation coefficients and linear regression statistics are unlikely to be sensitive to the addition and removal of mechanisms.
4. Examining distributional data with alternative indices of spatial structure may lead to a more intuitive understanding of how different mechanisms influence the form of abundance–occupancy relationships.

*Key-words:* aggregation, hypothesis testing, metapopulation structure, negative binomial distribution, spatial structure.

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A positive relationship between local abundance and regional occupancy (or range size) has been reported many times in the literature (e.g. Bock & Ricklefs 1983; Brown 1984; Gaston & Lawton 1990; Gaston 1994; Gaston 1996; Blackburn *et al.* 1997; Warren & Gaston 1997). In these studies, *abundance* is defined as the mean density of individuals in the habitat patches (or mapped grid squares) in which a species is present, and *occupancy* as the proportion of the total number of patches or squares that are occupied. The relationship is so widespread that it has been purported as one of the few general rules of ecology (Hanski, Kouki & Halkka 1993; Gaston 1994). Two recent papers (Gaston, Blackburn & Lawton 1997; Warren & Gaston 1997) have attempted to disentangle the influences of six biological explanations and two artefactual explanations for the positive relationship. However, neither paper gives serious

consideration to the null models developed by Wright (1991), reformulated and tested by Hanski *et al.* (1993), who illustrated that a positive relationship is the inevitable result of a range of theoretical spatial distributions of individuals. A restatement of Wright's work is helpful in the current context, as it is often confounded with (and dismissed along with) a separate sampling artefact described by Brown (1984), which only arises when there is systematic under-recording of rare species.

In the simplest case, where individuals of all species' populations are distributed at random, proportional occupancy ( $p$ ) and local abundance ( $a$ ) can be predicted from the zero-term of the Poisson distribution (Wright 1991).

$$p = 1 - e^{-\mu}, \quad \text{eqn 1}$$

$$a = \mu/p \quad \text{eqn 2}$$

Where  $\mu$ , the mean regional abundance (measured across the entire area including non-occupied

patches), will be different for each population. This biologically unlikely situation results in a highly rectilinear relationship between local abundance and regional occupancy typical of the 'high dispersal' plots of Fig. 3 in Warren & Gaston's (1997) microcosm experiment.

In reality though, individuals from most biological populations show aggregated distributions (Taylor, Woiwood & Perry 1978). Using the negative binomial distribution as a model, it is relatively straightforward to calculate the form of curvilinear relationship to be expected under conditions of greater aggregation. In all cases a positive relationship is generated (Wright 1991; Hanski *et al.* 1993). Figure 1 shows abundance–occupancy plots for four theoretical classes of populations. Within a class, populations have the same statistical spatial distribution of individuals, but each species–point has a different regional mean abundance,  $\mu$ . For a constant  $\mu$ , increasing aggregation (e.g. by restricting dispersal) moves points towards the top-left hand corner of an abundance–occupancy plot (cf. Figure 10.1 of Hanski *et al.* 1993; Warren & Gaston 1997)

There is little reason to suppose that rare species should exhibit markedly different levels of aggregation from common species (but see Cornell 1982; Taylor *et al.* 1978), therefore it is hardly surprising that positive correlations are commonly reported. Furthermore, if species' distributions vary from random to quite highly aggregated, then drawing a selection of points from these distributions will yield a triangular cloud of points. Such a pattern is commonly observed in abundance–occupancy plots (Gaston 1994; Warren & Gaston 1997) and is only weakly predicted by one of the biological mechanisms for generating positive correlations (Gaston *et al.* 1997).

This is not to say that the biological mechanisms

are unimportant; but in the chain of cause and effect it is the 'mechanisms' which generate spatial structure (e.g. aggregation), and sets of similarly aggregated populations result in positive correlations between abundance and occupancy. In the absence of any 'mechanism', random distributions result, but a positive correlation is still expected (Wright 1991). Therefore, if a positive relationship persists when a mechanism is removed, it does not imply that the mechanism was not contributing towards a particular form of positive relationship when it was present (Gaston 1996). In other words, contrary to Gaston *et al.* (1997) and Warren & Gaston (1997), none of the mechanisms predict 'no relationship' in their absence.

As the above discussion suggests, and as Warren & Gaston (1997) noted, simple correlation coefficients (or linear regressions) are an ineffective statistic for detecting system responses to the addition or removal of a single biological mechanism (in their case, metapopulation structure). Yet examination of their results suggest that the treatment did significantly alter the form of the abundance–occupancy relationship in a manner consistent with increasing spatial aggregation. Under such conditions, testing for deviations from a Poisson distribution might have been a more appropriate test (*sensu* Wright 1991). By logical extension, measuring differences in the mean level of aggregation, or some other index of spatial structure, would provide a sensitive and logical basis for comparative tests involving natural datasets, where many mechanisms may be acting in concert (e.g. Blackburn *et al.* 1997).

In short, abundance–occupancy relationships can best be understood as a simple measure of large-scale spatial structure (e.g. 'macro-aggregation'). The task for ecologists should now become an investigation of the relative influences of different biological mech-

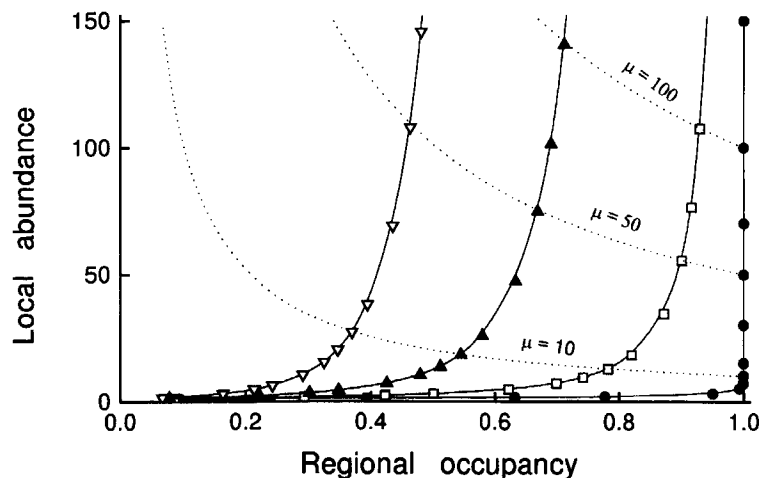


Fig. 1. The predicted relationship between local abundance and (mean expected) regional occupancy for sets of populations whose individuals show different degrees of aggregation in an eight-patch system. The parameter  $k$ , of the negative binomial distribution, assumes lower values as the degree of aggregation increases. (●) Poisson or random distribution, equivalent to  $k \rightarrow \infty$ . (□) Negative binomial,  $k = 0.5$ . (▲) Negative binomial,  $k = 0.2$ . (▽) Negative binomial,  $k = 0.1$ . Dashed lines indicate isolines of constant regional abundance,  $\mu$ .

anisms upon spatial structure *per se*, and from this an understanding of how abundance–occupancy plots vary, will naturally follow. In this sense, spatial structure need not necessarily be measured by  $k$  of the negative binomial as other indices have their own advantages and disadvantages (see Bliss & Fisher 1953; Southwood 1978; Taylor *et al.* 1978; Hulbert 1990; Legendre 1993). The negative binomial model was used in the present study because it allows one to make specific predictions of occupancy and local abundance for any given combination of  $\mu$  and  $k$  (see Fig. 1).

Further applications of the general approach advocated here can easily be imagined. For example, one could test Cornell's (1982) prediction that rare species may be more clumped than common species (although admittedly, his model is based on rather small-scale mechanisms). If the latter prediction is true, then it would actually counteract the tendency for abundance–occupancy relationships always to be positive. As a general rule of ecology, the positive relationship between abundance and occupancy is worthy of attention, but it is also worthy of more discerning methods of description and analysis.

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### Appendix 1

#### EQUATION FOR GENERATING ABUNDANCE–OCCUPANCY RELATIONSHIPS WITH A NEGATIVE BINOMIAL DISTRIBUTION

Note that in the original paper by Wright (1991) the formula for calculating proportional occupancy ( $p$ ) from a negative binomial distribution was accidentally published with a division sign ( $\div$ ) in place of an addition sign ( $+$ ). Thus, the correct equation is given below.

$$p = 1 - \left(1 + \frac{\mu}{k}\right)^{-k} \quad \text{eqn A.1}$$

Where  $\mu$  is the mean abundance (across all sites or patches) and  $k$  is the clumping parameter of the negative binomial distribution. The value of  $k$  can be calculated for empirical data sets using a maximum likelihood approach (Bliss & Fisher 1953; Southwood 1978), and in small-scale biological situations values are usually found to lie in the range 0.1–4 (Rosewell, Shorrocks & Edwards 1990; Jaenike & James 1991; Wright 1991; and references therein).