



## Notes

## Length-based connectivity metrics and their ecological interpretation

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## ABSTRACT

Metrics that quantify habitat connectivity and fragmentation in landscape ecology are examined, as well as the relations between them and their interpretation. The radius of gyration, defined here as the root-mean-square distance of habitat patches from the centre of the habitat, has special significance from an ecological point of view that other metrics lack. This metric has been incorrectly used in the field of landscape ecology – its definition is different from its definition in every other field, causing it to lose its ecological meaning. Inconsistencies in terminology between landscape ecology and other fields raise dangers of misinterpretation of metrics.

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## 1. Introduction

Habitat change is a key driver of biodiversity loss (Duraiappah et al., 2005) and quantifying how land use change influences habitat connectivity and fragmentation is a challenging problem in landscape ecology. A huge number of landscape metrics exist (Wu, 2013). Many of these are convenient to measure and are capable of identifying patterns in landscapes, but are unable to relate these patterns to underlying processes (Ewers and Didham, 2007; Kupfer, 2012; Moilanen and Hanski, 2001). The relationship between particular metrics and changes in a landscape has been previously addressed (Hargis et al., 1998), but a clear ecological interpretation is not available for every common metric, while the use of metrics without a clear ecological relevance can lead to meaningless results (Li and Wu, 2004; White et al., 2014). The availability of software to facilitate computing landscape metrics, such as the widely used FRAGSTATS package (McGarigal et al., 2012) has greatly empowered ecologists and geographers, but raised the possibility of inappropriate use of quantitative data, and especially of misinterpretation of the ecological significance of measurements.

One metric in particular has been misused in the ecological literature, the ‘radius of gyration’. Keitt et al. (1997) and Riitters et al. (1995) were early users in ecology of what they describe as the radius of gyration, but the equations given differ from one another and neither coincides with the definition of radius of gyration that

is in use everywhere except in landscape ecology. The radius of gyration was originally a physics term, used as a measure of the distribution of mass of an object (Synge and Griffith, 1959). Keitt et al. (1997) give two ecological interpretations of the metric, but neither of them corresponds to any definition of the radius of gyration. However, if the radius of gyration is calculated correctly, it can give a meaningful measurement of an animal’s dispersal within a habitat patch.

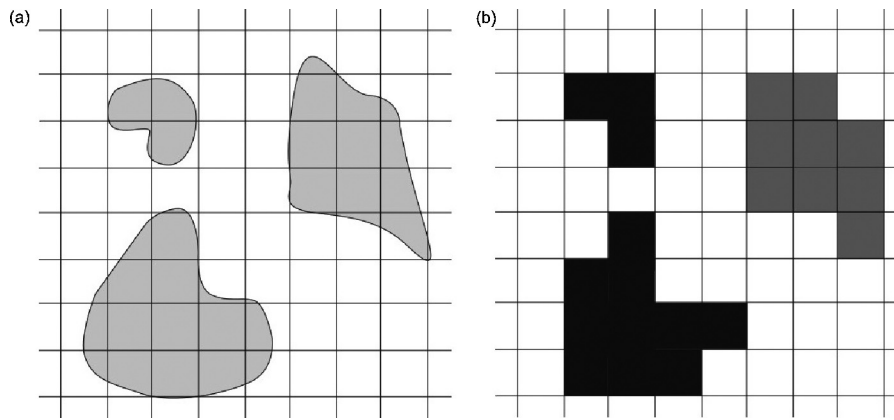
In this note, we discuss six landscape metrics with the units of length, as length metrics are suitable for calculating dispersal range (which is by definition a length). One of these is included in FRAGSTATS as the statistic GYRATE, but all are readily computable from categorical maps. We address the relations between these six distance measures and their ecological significance, and in particular the difference between GYRATE and ‘radius of gyration’ that arises in other disciplines. We also consider a potentially ecologically relevant landscape metric that standard software is unlikely to deliver, based on the time taken for a randomly exploring animal to reach the edge of its allowed habitat, which produces a distance metric quite distinct from the others discussed here.

## 2. Six distance scales for discrete data

In this section we consider six landscape metrics that can be easily calculated. We show how they are derived and why they are potentially useful. Finally, we show that only two of these metrics are related, producing an ecological interpretation for the radius of gyration. Meaningful landscape metrics (e.g. to characterize habitat configuration) should be free from any dependence on choices of origin of coordinates or idiosyncrasies in definitions. It is natural,

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**Fig. 1.** Habitat regions and their discrete representation. (a) The smooth grey regions represent suitable habitat for a species. (b) The centres of the shaded squares define the discrete habitat points, which may be characterized quantitatively en masse, or by first computing metrics for the clusters separately, and then constructing a cluster-size weighted average. Depending on the ability of the species under study to migrate across inhospitable territory, the three clusters could be appropriately analysed as a single habitat, or as two habitats (both black clusters as one habitat, and the dark grey cluster as a second, distinct habitat), or as three distinct habitats.

therefore, to compute metrics that arise from some form of average of distances of arbitrary points from the centre of the habitat, from the nearest boundary of the habitat, or in relation to the rest of the habitat. We discuss all of these below. Appendix A contains a discussion of these matters for continuous regions, whereas in this section we address discrete landscape data. For example, discrete data arises by covering the landscape with a regular grid (say a square mesh) and identifying the central point of a mesh cell that is filled with habitat (either completely, or to a specified fraction) as a discrete habitat point, which we refer to as a *patch*. This process of altering continuous regions to discrete landscape data is illustrated in Fig. 1.

If our discrete habitat consists of  $N$  points ( $\mathbf{r}_i$ , where  $1 \leq i \leq N$ ) then the *centroid* or *centre of mass* of the habitat is given by

$$\mathbf{r}_{cm} = (x_{cm}, y_{cm}) = \frac{1}{N} \sum_{i=1}^N \mathbf{r}_i. \tag{1}$$

By analogy with conventional use in other disciplines, we define the *radius of gyration*  $R_g$  by

$$R_g^2 = \frac{1}{N} \sum_{i=1}^N |\mathbf{r}_i - \mathbf{r}_{cm}|^2. \tag{2}$$

The term radius of gyration has its roots in physics, where both the discrete system equations (1) and (2) and their continuum analogues (discussed in Appendix A) arise. For a rigid body, the ratio of the moment of inertia about an axis to the total mass of that body is the square of the radius of gyration about the axis (Syngue and Griffith, 1959). The moment of inertia determines the torque required to rotate the body with a specific angular acceleration. Eq. (2) corresponds to the definition of the radius of gyration for a rigid assembly of point masses (each with the same mass). This definition also agrees with that used in statistical physics in the context of the shape of random walks Hughes (1995) and percolation clusters (Hughes, 1996; Stauffer and Aharony, 1994).

The radius of gyration can be calculated for objects in an arbitrary number of dimensions, but in the context of landscape metrics, we are interested in the two-dimensional case. For this special case, the radius of gyration is a natural length that characterizes the extent of a region:  $R_g$  is the root-mean-square (RMS) distance between habitat patches and the habitat centroid. Although the radius of gyration can be used directly whether or not the habitat is connected, if the total habitat consists of disconnected clusters, a finite number of isolated habitat clusters may be

identified. If a habitat cluster contains  $N(k)$  patches, where  $k$  is the cluster's label, and has radius of gyration  $R_g(k)$ , then an appropriate area-weighted average of the radii of gyration of the distinct habitats, perhaps naturally called the *correlation length* by analogy with statistical physics, is the length-scale  $\xi$  defined by

$$\xi^2 = \frac{\sum_k R_g(k)^2 N(k)}{\sum_k N(k)}. \tag{3}$$

If precedents in other disciplines are ignored, a plausible different measure of the typical distance of habitat points from the centroid is

$$R_* = \frac{1}{N} \sum_{i=1}^N |\mathbf{r}_i - \mathbf{r}_{cm}|. \tag{4}$$

Here, and in subsequent discussion, a subscript asterisk on a parameter indicates that it is computed as a direct average, rather than as an RMS average. The FRAGSTATS package statistic GYRATE corresponds to  $R_*$ . For fragmented habitats, the analogue of Eq. (3) is

$$\xi_* = \frac{\sum_k R_*(k) N(k)}{\sum_k N(k)}. \tag{5}$$

In FRAGSTATS notation,  $\xi_* = \text{GYRATE\_AM}$ .

For any random variable  $X$  with finite variance, the inequality  $\langle (X - \langle X \rangle)^2 \rangle \geq 0$  (where angle brackets denote expectation) ensures that  $\langle X^2 \rangle \geq \langle X \rangle^2$ , with equality only possible in the trivial case where  $X$  takes a unique value with probability 1. Hence (excluding the trivial case of a habitat with only one patch), we have the strict inequality  $R_g > R_*$ . The discrepancy between  $R_g$  and  $R_*$  is illustrated in Fig. 2: it is quite sensitive to how the patches are arranged.

Another way to characterize habitat connectivity is to average in some way the separation of randomly chosen patches. To this end one may introduce the root-mean-square patch separation  $\rho$  and the mean patch separation  $\rho_*$  defined by

$$\rho^2 = \frac{1}{N^2} \sum_{i=1}^N \sum_{j=1}^N |\mathbf{r}_i - \mathbf{r}_j|^2; \tag{6}$$

$$\rho_* = \frac{1}{N^2} \sum_{i=1}^N \sum_{j=1}^N |\mathbf{r}_i - \mathbf{r}_j|. \tag{7}$$

In addition to noting the strict inequality  $\rho > \rho_*$  for discrete non-trivial habitats, we draw to the reader's attention the easily proved

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