Global Ecology and Conservation 6 (2016) 93–104

Contents lists available at ScienceDirect

Global Ecology and Conservation

journal homepage: www.elsevier.com/locate/gecco

Original research article

The Modifiable Conceptual Unit Problem demonstrated using pollen and seed dispersal

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A R T I C L E   I N F O

Article history:
Received 22 November 2015
Received in revised form 12 February 2016
Accepted 13 February 2016
Available online 9 March 2016

Keywords:
MAUP
Spatial
Conceptual
Grid
Dispersal
Pollen

A B S T R A C T

The Modifiable Areal Unit Problem (MAUP) is a famous issue in spatial analysis that states the output of a spatial analysis is influenced by the spatial extent of the units used in the analysis. This study demonstrates that the MAUP is accompanied with another intractable spatial issue in spatial modeling; the Modifiable Conceptual Unit Problem (MCUP). The MCUP states that the conceptualization of spatial processes impacts the output of spatial analysis and occurs when a model with one spatial dimension is applied to a spatial model with more than one spatial dimension. This study demonstrates the MCUP by developing three conceptual models of dispersal and showing how they produce different results even when given the same initial dispersal curves and areal units. Three conceptual models of dispersal (*sum of curve points* model, *area of distance range* model, and the *volume of distance range* model) are described and applied to a grid landscape with a single point of dispersal and a grid landscape with multiple points of dispersal. A Geographic Information System (GIS) is used to evaluate how the models differ in their distribution of pollen or seeds across the landscapes. The three models of dispersal are each valid conceptualizations of the dispersal process, but when given the same dispersal curve parameters, they produce different distributions of dispersed items across grid landscapes. The *sum of curve points* model is the least complicated model because it only uses a few points from the defined dispersal curve. The *area of distance range* model uses the entire dispersal curve, but is based on a single dimension of space and thus conceptually abstracted from the grid landscape. The *volume of distance range* model uses the two spatial dimensions present in the grid landscape and thus is the most conceptually sound model of the three. The underlying conceptualization of the dispersal process can impact the results of dispersal models. Applying dispersal curves with one spatial dimension to grids with two spatial dimensions makes inherent assumptions about the conceptualization of dispersal. This study highlights the necessity of researchers to declare their conceptual models of dispersal when applying modeled dispersal curves to grid landscapes.

1. Introduction

1.1. Areal units and conceptual units

A fundamental tenant of spatial analysis is that the spatial units used in an analysis are "arbitrary with respect to the phenomena under investigation, yet the aggregation units used will affect statistics determined on the basis of data reported

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http://dx.doi.org/10.1016/j.gecco.2016.02.003
2351-9894/

in this way'' (O'Sullivan and Unwin, 2003). This issue underlies any spatial analysis that aggregates phenomena in space and is known as the Modifiable Areal Unit Problem (MAUP). The MAUP issue is well documented and is a foundational consideration in the spatial analyses of any discipline whether it is explicitly discussed (Jelinski and Wu, 1996; Dark and Bram, 2007) or implicitly considered (Saura and Martinez-Millan, 2001; Wu et al., 2002). While the problem of aggregation in spatial units has become established in the academic literature through the MAUP, a related issue regarding the conceptualization of dispersal across spatial units has not been developed. This study introduces the problem of conceptual units in spatial analysis (the Modifiable Conceptual Unit Problem; MCUP) through the development of three models of dispersal that use different conceptual units to represent the dispersal process.

An areal unit is easily understood through the consideration of a tile floor. If we cover the floor with square tiles, we see an entire space broken into equally sized parts. We also recognize that we can make patterns or images by changing the color of some of the tiles. The key to understanding the MAUP in this example is recognizing that the size of the tiles impacts the nature of the patterns or images that can be made. As tile size decreases, more details can be expressed in the patterns or images. As tile size increases, the smaller tiles are aggregated within the larger tiles, thus changing the nature of the patterns or images. To understand the nature of a conceptual unit, we can think of a water sprinkler in the same tiled room. If we assume a dispersal curve that decreases the amount of water dispersed as distance from the sprinkler increases, we produce a model of dispersal that has the amount of water dispersed on the y-axis and distance from the sprinkler on the x-axis. The problem we have is that the tiled room has two spatial dimensions while our dispersal model only has one spatial dimension. A conceptual unit is the way we apply the dispersal curve with one spatial dimension to the tiled floor that has two spatial dimensions.

While the example of a tiled room and a sprinkler is useful for understanding the natures of areal and conceptual units, it fails to communicate the real-world implications of the MAUP and the MCUP. Whereas the MAUP has already been established as foundational to spatial analysis in the academic literature (Jelinski and Wu, 1996; Saura and Martinez-Millan, 2001; Wu et al., 2002; O'Sullivan and Unwin, 2003; Dark and Bram, 2007), the MCUP is a new consideration that has important consequences for any theoretical or applied dispersal analysis. This study uses the existing ecological literature regarding pollen and seed dispersal to demonstrate the existence and importance of the MCUP by developing three models of dispersal that use different conceptual units and thus produce quantitatively different results.

1.2. Modeling dispersal

Although the process of dispersal has a vast literature in both population genetics and landscape ecology, particularly for the dispersal of pollen and seeds, the estimates of pollen and seed dispersal distances vary widely, even between species in the same genus. Estimates of pollen dispersal for pine species range from well under a hundred meters to many thousands of meters (Wright, 1952; Wang et al., 1960; Lindgren et al., 1995; Marquardt and Epperson, 2004; Robledo-Arnuncio et al., 2006). Pine seeds also have a considerable range of dispersal distance estimates (Epperson and Allard, 1989; Nathan et al., 2000; Gonzalez-Martinez et al., 2002; Vander Wall, 2003; Grace et al., 2004). These wide ranges of dispersal distances suggest that the landscape contexts of the studies may be important factors in the observed characteristics of dispersal. In order to understand dispersal at the landscape level, the estimates of pollen and seed dispersal, as modeled with mathematical representations of dispersal, need to be applied to representations of landscapes. A Geographic Information System (GIS) provides the platform which can apply models of dispersal to landscapes and help integrate the process of dispersal with the patterns of species locations in landscapes. This study develops conceptual models of dispersal, which is a prerequisite to the use of GIS to model dispersal through real landscapes.

Most studies of pollen and seed dispersal follow one of three methodologies: ecological observation, genetic analysis, and dispersal modeling. Ecological observation studies have included using pollen and seed traps (Wright, 1952; Wang et al., 1960; Nathan et al., 2000; Hewitt and Kellman, 2002), tracking dispersed items (Iida, 1996; Pons and Pausas, 2007), and observation of dispersers and offspring (Johnson, 1988; Lindgren et al., 1995; Gomez, 2003). Genetic analysis studies of dispersal use the relationships between individuals to develop estimates of dispersal curves and distances for pollen and seeds (Shen et al., 1981; Dow and Ashley, 1998; Streiff et al., 1999; Gonzalez-Martinez et al., 2002; Grace et al., 2004; Austerlitz et al., 2007). Dispersal modeling studies broadly examine mathematical representations of dispersal and how they can be impacted by various environmental factors (Okubo and Levin, 1989; Malanson and Armstrong, 1996; Meagher et al., 2003; Smouse and Sork, 2004; Schueler and Schlunzen, 2006; Williams et al., 2006; Kuparinen et al., 2007; Snall et al., 2007).

Ecological observation studies look directly at the dispersed objects (e.g. Wright, 1953, Iida, 1996 and Vander Wall, 2003) or evidence of object movement, such as pollination due to the transport of pollen grains (Lindgren et al., 1995). These types of studies typically describe dispersal through the development of dispersal curves (Wright, 1952, 1953; Wang et al., 1960; Johnson, 1988; Nathan et al., 2000), or distance-based descriptions of movement (Lindgren et al., 1995; Iida, 1996; Hewitt and Kellman, 2002; Vander Wall, 2003; Pons and Pausas, 2007). The dispersal curves provide a quantification of the dispersed objects along a distance axis (with the height of the curve representing the amount of dispersant transported a certain distance from the point of origin, while the studies with distance-based descriptions typically only provide an average distance of dispersal and observed dispersal distance limits). Even though the distance-based descriptions help conceptualize the limits of dispersal over space, the dispersal curves are more useful for modeling how a total amount of dispersal objects is partitioned to the space around the origin of dispersal. Conceptually, the dispersal curves model an even dispersal of objects based on a mathematical equation, while distance based descriptions are used to describe clumped or