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Rectangular and hexagonal grids used for observation, experiment and simulation in ecology

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ABSTRACT

Regular grids or lattices are frequently used to study ecosystems, for observations, experiments and simulations. The regular rectangular or square grid is used more often than the hexagonal grid, but their relative merits have been little discussed. Here we compare rectangular and hexagonal grids for ecological applications. We focus on the reasons some researchers have preferred hexagonal grids and methods to facilitate the use of hexagonal grids. We consider modelling and other applications, including the role of nearest neighbourhood in experimental design, the representation of connectivity in maps, and a new method for performing field surveys using hexagonal grids, which was demonstrated on montane heath vegetation.

The rectangular grid is generally preferred because of its symmetrical, orthogonal co-ordinate system and the frequent use of rasters from Geographic Information Systems. Cells in a rectangular grid can also easily be combined to produce new grids with lower resolutions. However, efficient co-ordinate systems and multi-resolution partitions using the hexagonal grid are available. The nearest neighbourhood in a hexagonal grid is simpler and less ambiguous than in a rectangular grid. When nearest neighbourhood, movement paths or connectivity are important, the rectangular grid may not be suitable. We also investigate important differences between visualizations using hexagonal and rectangular grids. A survey of recent uses of grids in Ecological Modelling suggested that hexagonal grids are rarely used, even in applications for which they are more suitable than rectangular grids, e.g. connectivity and movement paths. Researchers should consider their choice of grid at an early stage in project development, and authors should explain the reasons for their choices.

1. Introduction

Regular grids are frequently used by ecologists in various ways. Regular patterns are the most efficient in several respects for surveys, sampling and experimental planting arrangements (Olea, 1984; Dale, 1998). Long, thin quadrats usually minimize the variance between quadrats (Clapham, 1932; Krebs, 1989), suggesting conversely that regular polygons in arrays are most efficient for mapping spatial variation (Dale, 1998). Remotely sensed data are stored as pixels in regular lattices. Thus regular lattices are important for experimental and observational science, as well as providing the most common framework for spatially explicit models (Table 1).

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Table 1 – Summary of papers in Ecological Modelling vol. 195–199, in relation to whether they were spatial and whether they used grids or alternative methodologies

Type of spatial model	Number of papers	Mapping or GIS only	Includes spatial interactions	Includes nearest neighbour interactions
Total number of papers	209	–	–	–
Non-spatial paper	108	–	–	–
Spatial paper	101	27	64	–
One dimension only	15	3	9	–
Continuous space	10	1	5[a]	–
Metapopulations	9	1	6	–
Grid	67	22	44	31
Square/rectangular	64	21	42	29
Hexagon	2	0	2	2
Unspecified	1	1	0	0

"–" indicates that the question was not considered relevant to the type of spatial model.

[a] Three of the papers considering spatial interactions in continuous space were three-dimensional canopy simulations. Only two were comparable with dynamic models in grids (Tyre et al., 2006; Zhao et al., 2006).

Many ecological models contain spatially explicit representations of the environment, because some ecological processes depend on the position of ecological entities in their environments (Durrett and Levin, 1994; Berec, 2002). Such processes include dispersal, local competition, social and territorial behaviour, and the impacts of spatial heterogeneity. However, although the type of object representation of entities has been considered (cellular automata, coupled map lattices, individual-based models and interacting particle systems) (DeAngelis and Rose, 1992; Berec, 2002), relatively little thought has been paid to the representation of space and the co-ordinate system used by models (Keeling, 1999).

There are three regular tessellations of a plane: hexagons, squares and triangles (Carr et al., 1992). The triangular tessellation requires the triangles to have two different orientations, so its unpopularity is understandable (except in geodesic discrete global grids (Sahr et al., 2003)). However, it is less clear why the square tessellation or rectangular grid is used in ecology so much more frequently than the hexagonal tessellation (Table 1). The hexagonal tessellation has been used for a long time: Sakai (1957) used a hexagonal experimental arrangement, while Weiner and Conte (1981) used a hexagonal grid for simulation. In contrast, once introduced, hexagonal grids rapidly replaced rectangular grids on commercial military game maps nearly 40 years ago, and persist in many computer games (Palmer, 1977; Dunnigan, 1992). The purpose of this paper is to compare these two grids and their strengths and weaknesses. Although the grids are labelled "rectangular" and "hexagonal" after the shapes of their polygonal elements, the lattices, i.e. the spatial arrangement of the polygons, are also important. The hexagonal grid is actually arranged on a equilateral triangular lattice, or "hexagonal" lattice, which is the most compact arrangement of many equal circles.

This paper only considers a small part of the range of options for tessellating or tiling a plane (Grünbaum and Shephard, 1987). For example, simulations could use irregular tessellations, mixing two or more different polygons, possibly arranged in non-repeating patterns (Penrose, 1974). Alternatively tessellations may change with time, being dependent on the current distribution of entities (Okabe et al., 1999). Neighbourhoods can be defined arbitrarily without a geometric basis, for example when administrative boundaries (e.g. counties, postcodes) are used. Individual-based models can avoid using tessellations by operating in continuous space (Blackwell, 1997; Weiner et al., 2001). However, use of the rectangular grid is so predominant that we focus on comparison with the closest alternative, the hexagonal grid. We start with a survey of recent publications, which confirms the dominance of the rectangular grid. Recognising that hexagonal grids are potentially useful to all ecologists, we will then consider applications of hexagonal grids in survey, sampling and experimental design, before considering their applications in modelling.

2. A study of the current use of grids

The application of grids is so frequent and routine that it is often unstated: their presence may be implicit rather than explicit even in the methods sections of scientific papers. Therefore only an unrepresentative minority of papers using them can be identified by using keyword searches on literature databases. Instead, we obtained a contemporary view of the use of grids by examining every paper published in volumes 195–199 of Ecological Modelling, the second half of 2006 (Table 1). Papers were identified as being spatial if spatial location (not just local environment) had a clear role in the patterns, processes or methods they described. Spatial papers were classified as "mapping only", if they discussed the generation of maps or GIS rasters, but included no spatial interactions. Nearest neighbour interactions could only occur in spatial grids, being defined as any process or calculation involving only the cells adjoining or touching a target cell in a grid.

Ecological Modelling was selected as a journal likely to have a high proportion of papers that were spatial and considered spatial interactions. Nearly half of the 209 papers examined were spatial, while 64 included spatial interactions (Table 1). Rectangular grids were the dominant spatial model, including 64 of the spatial papers and 42 of the papers with spatial interactions. The 44 papers presenting spatial interactions using grids are listed and classified in Table 2.

Table 2 – Papers from Ecological Modelling vol. 195–199 using spatial grids and including interactions between grid cells

Application	Number of papers	Biotic movement	Nearest neighbourhood	Distant interactions	References
Using GIS rasters	19				
Hydrodynamic model with model of wigeongrass spread	1	Y	0	Y	Giusti and Marsili-Libelli (2006)
Mussel continuous movement	1	Y	Wt.	Y	Morales et al. (2006)
Frog cell-based movement	1	Y	?	N	Boone et al. (2006)
Tree beetle spread	1	Y	8	Y	BenDor et al. (2006)
Smoke spread	1	N	0	Y	McKenzie et al. (2006)
Ecohydrology: source cell to stream calculation	1	N	0	Y	Kokkonen et al. (2006)
Ecohydrology: flow route traced cell by cell	2	N	?	Y	Apaydin et al. (2006) and Hattermann et al. (2006)
Incorporating neighbourhood effects into cell environment	3	N	0	Y	Ashcroft (2006), Holzkämper et al. (2006) and Lobell and Ortiz-Monasterio (2006)
Incorporating neighbourhood effects into cell environment at global scale	1	N	8	N	Stockwell et al. (2006)
Neighbourhood effects including least cost distances	2	N	8	Y	McNeil et al. (2006) and Ray and Burgman (2006)
Hydrodynamics calculated using partial differential equations (PDEs)	3	N	4	N	Lopes and Silva (2006), Monte et al. (2006) and Na and Park (2006)
Snow movement	1	N	4	Y	Hiemstra et al. (2006)
Effect of land cover change on hydrology	1	N	8	N	Samaniego and Bárdossy (2006)
Other rectangular grids	23				
Seed or animal dispersal	7	Y	0	Y	Arii and Parrott (2006), Hilker et al. (2006), Lischke et al. (2006), Lischke and Löffler (2006), Mildén et al. (2006), Münkemüller and Johst (2006) and Robinson and Geils (2006)
Seed dispersal, variable range	1	Y	8	Y	Eppstein et al. (2006)
Biotic dispersal, continuous range within grid environment	1	Y	8	Y	Potthoff et al. (2006)
Seed dispersal, continuous range and vegetative growth	1	Y	4	Y	Reineking et al. (2006)
Grazing experiment	1	Y	4	Y	Walker et al. (2006)
Abstract spatial population dynamics	1	Y	4	Y	Ezoe and Nakamura (2006)
Fishing model with elementary hierarchical design	1	Y	4	Y	Dreyfus-Leon and Gaertner (2006)
Oceanic fish movements calculated by coupled PDEs	1	Y	4	N	Sundermeyer et al. (2006)
Coral reef dynamics	1	Y	4	N	Mumby et al. (2006)
Dispersal of disease, parasitoids and algal blooms	3	Y	8	N	Chen and Mynett (2006), Monteiro et al. (2006) and Nguyen-Huu et al. (2006)
Vegetation dynamics	1	Y	?	Y	Tews et al. (2006)
Aphid dispersal, continuous range within grid environment	1	Y	Wt.	Y	Parry et al. (2006)
Fire, wind damage in forests	2	N	4	N	Barclay et al. (2006) and Schlicht and Iwasa (2006)
Nutrient dynamics in the vertical plane in water, PDEs	1	N	4	N	Komatsu et al. (2006)
Hexagonal grid for self-organizing maps generated by artificial neural networks	2	N	6	N	Gevrey et al. (2006) and Park et al. (2006)

The table presents for each set of papers a brief statement of the relevant spatial process, whether biotic movements are represented (Y = yes, N = no), the number of nearest neighbours (0 = no nearest neighbour process, 4 = 4 neighbourhood, 8 = 8 neighbourhood, Wt. = diagonal and orthogonal neighbours given different weight, ? = insufficient information in paper to determine nearest neighbourhood), whether distant interactions beyond nearest neighbours occur, and references to the papers in the set.

Geographical Information System (GIS) rasters and remote sensing make a large contribution to the current dominance of rectangular grids, including 41 of the spatial papers in this survey (Tables 1 and 2). However, these included 22 of the 23 spatial papers with grids that did not include spatial interactions (Table 1). Moreover, only 4 out of 19 papers investigating spatial interactions using GIS rasters consider biological movements or spread (BenDor et al., 2006; Boone et al., 2006; Giusti and Marsili-Libelli, 2006; Morales et al., 2006), suggesting that the merging of GIS tools with biological and dynamic modelling is far from complete (Table 2). In contrast, 20 out of 23 papers using other rectangular grids to study spatial interactions investigated dispersal or other biological movements. Thus rectangular grids dominate modelling of spatial biodynamics in ecology, even after excluding GIS rasters. Hexagonal grids are only represented by self-organizing maps (Gevrey et al., 2006; Park et al., 2006), which are a visualization tool with a very abstracted relationship with spatial location. However, hexagonal grids would have been suitable for several other papers, as will be discussed below.

Nearest neighbour processes or calculations were presented in 31 of the 44 papers with grids and spatial interactions (Table 1), but 8 of the 13 papers avoiding nearest neighbour processes included biological dispersal (Table 2). This suggests that researchers were not comfortable with the rectangular grid geometry, so they deliberately used fine grids to make their dispersal models more like models in continuous space. This is potentially inefficient and misses opportunities to exploit the geometric properties of the grid (Birch, 2006). There were also several models combining an individual-based model (IBM) of organisms in continuous space with an environmental model based on a rectangular grid (e.g. Morales et al., 2006; Parry et al., 2006; Reineking et al., 2006), which risk having their accuracy determined by the grid rather than the IBM.

3. Survey and sampling

3.1. *Sampling*

Maps of many field measurements require interpolation from values observed at scattered sample points. For a given number of sample points, sampling from regular lattices maximizes the precision of spatial functions estimated by kriging (Olea, 1984). The hexagonal lattice is slightly more regularly spaced than the regular rectangular lattice: points in a hexagonal lattice are 7.5% farther from their nearest neighbours than points in a square lattice at equal density. However, differences between kriging estimates using the hexagonal grid and the rectangular grid are trivial compared with the differences between either regular grid and more irregular sampling patterns (Olea, 1984).

Currently the most popular sampling grid for sampling large areas is a rectangular grid based on latitude and longitude. However, grids defined by latitude and longitude are inadequate for global coverage, or for any area large enough to be significantly affected by global curvature (Sahr et al., 2003). Sampling of very large areas, such as the EMAP coverage of the USA, is increasingly being based on geodesic discrete global grids, in which grid cells are as likely to be hexagons as squares (Hale et al., 1998; Sahr et al., 2003).

Hexagons have some advantages from being closer in shape to circles than are squares. Thus a hexagon has a shorter perimeter than a square of equal area, which potentially reduces bias due to edge effects (Krebs, 1989). A square with unit area has a perimeter with length 4, whereas the perimeter of a hexagon with unit area is 3.722, so the edge to area ratio of a hexagon matches that of a square with 15.5% more area. Rempel et al. (2003) considered this small difference sufficient to recommend hexagonal sampling grids. Also, some parts of a square are farther from its centre than any part of a hexagon of equal area, so the average distance from the centre of a square with unit area is 0.3826, whereas the average distance from the centre of a hexagon with the same area is 0.3772. This difference could be equalized by covering an area with just 2.9% more squares than hexagons. Nevertheless, Overton et al. (1990) presented these small quantitative advantages, along with "an extra degree of freedom from coincidence with anthropogenic structures", as being the reasons for preferring a hexagonal grid for the Environmental Mapping and Assessment Project (EMAP) in the USA. The EMAP data set is based on a random systematic hexagonal grid identifying 12,600 locations at 27 km intervals nationwide (Hunsaker et al., 1994; Hale et al., 1998).

3.2. *Field survey*

Here we distinguish survey from sampling by considering survey to be the observation of measures, such as vegetation cover, over a whole area. Dale (1998) believed hexagonal quadrats provided few advantages for field observations compared with the extra difficulty of laying them out. However, many of the advantages from using hexagonal grids in surveys are due to arranging quadrats in a hexagonal lattice, rather than the hexagonal quadrat itself. The gaps between rows in a hexagonal lattice are $\sqrt{3}/2$ (ca. 0.866) of the distance between neighbouring lattice points. Therefore, oblong quadrats with height $\sqrt{3}/2$ of their length tessellate as a hexagonal lattice (Fig. 1). Each oblong would share over 91% of its area with a hexagon of equal area sharing the same centre. Thus a hexagonal lattice of oblong quadrats may be an adequate surrogate for a hexagonal grid. In a rectangular array of quadrats, groups of four or nine adjacent quadrats can be aggregated to generate a coarser grid with double or triple the grid-spacing. Equivalent aggregation in a hexagonal lattice requires recording of each original quadrat as left and right halves, so that half quadrats can be used for composition (Fig. 1). Thus, a rectangular grid of oblongs with height $\sqrt{3}$ times their width can be used to survey for a hexagonal grid map (Fig. 1).

To test the feasibility of field survey using a hexagonal lattice of oblong quadrats, we surveyed an area ca. $3\,m \times 3\,m$ of banded prostrate montane heath (H13 *Calluna vulgaris–Cladonia arbuscula* heath in Rodwell (1991)) at an altitude of 750 m on a ridge of Culardoch in the Grampian mountains of Scotland (Ordnance Survey grid reference no. 184985). We used a 14×12 array of quadrats $0.233\,m \times 0.269\,m$ (area = $0.0625\,m^2$). Preparation, consisting of laying out markers and string to indicate rows, required 10 min longer than for

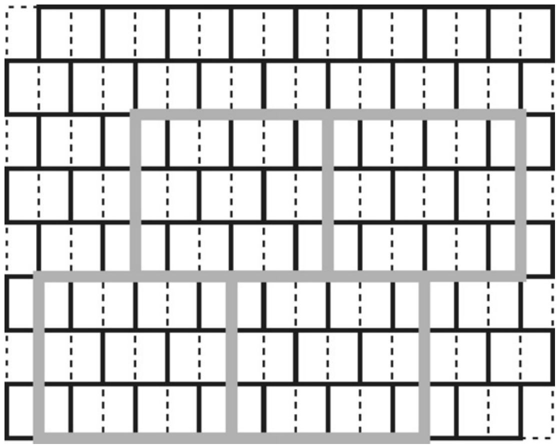

Fig. 1 – A design for performing a field survey based on a hexagonal grid. Narrow dashed lines are a rectangular grid of oblongs with width 1 unit and height $\sqrt{3}$ units. Solid dark lines are oblongs width 2 units, height $\sqrt{3}$ units superimposed on the rectangular grid of smaller oblongs. Alternate rows of the dark oblongs are offset, so that their centres are arranged as a hexagonal lattice and the outlines of the oblongs approximate a hexagonal grid. The widest, grey lines indicate four larger oblongs, each containing nine (seven whole and four halves) of the smaller oblongs. The larger oblongs also form a hexagonal lattice aligned with the more fine-grained lattice.

a 13 × 13 array of square quadrats 0.25 m × 0.25 m. There was no difference in the time required for recording the quadrats themselves (5.5 h). Therefore survey using a hexagonal lattice increased preparation time by about 50% and total survey time by about 3%.

Oblong quadrats in the hexagonal lattice were recorded as left and right halves (Fig. 1), which allowed four visualizations of the same observations, including a rectangular grid and a hexagonal grid (Fig. 2). The details of the vegetation are not of immediate interest here, but the maps provide an opportunity to compare the same patterns in hexagonal grid maps and rectangular grid maps. The visual advantages of hexagon grid maps may be greater than their advantages in accuracy (Carr et al., 1992):

1. Maps in a hexagonal grid tend to be less ambiguous than maps in a rectangular grid. The rectangular grid map is ambiguous where similar cells meet at corners, not edges. For example, near the labels “A” and “B”, diagonal pairs of cells with relatively high cover of *C. vulgaris* cross pairs of cells with lower cover of *C. vulgaris* (Fig. 2b). Above and to the left of A and B, patches of low *C. vulgaris* cover may be isolated by a barrier of high cover. Below B, a cell with high *C. vulgaris* cover may be surrounded by low cover. In contrast, in Fig. 2c and d the patch of low cover left of A is clearly isolated, the low cover above and to the left of B is only partly isolated by a cell with intermediate cover, while the cell of high cover below B is clearly isolated. Whether an ambiguous visualization is preferable will be context dependent (compare with Fig. 2a).
2. The grid lines in rectangular grid maps are straight, unbroken, vertical and horizontal lines crossing the surface. Their continuity tends to merge orthogonally neighbouring cells, which may or may not be desirable (Fig. 2a–c). They are also distracting because human vision is especially sensitive to vertical and horizontal lines (Coppola et al., 1998).
3. Cells in a hexagonal grid are aligned along three axes rather than just two, so the outlines of groups of cells in a hexagonal grid form more varied, less rectilinear shapes than groups of cells in a rectangular grid (Overton et al., 1990).

4. Experimental design

Monocultures of multiple plants are routinely planted in regular arrays for controlled experiments. For this purpose, the differences between rectangular grids and hexagonal grids may be minor, except the rectangular grid more often matches the shapes of plots or boxes available for experiments.

Planting patterns may matter more when contrasting plants are intermixed. Abstract models and simulations based on field calibration indicate that the spatial distribution of plants should strongly affect their interactions (Pacala and Levin, 1997; Bolker et al., 2003). Natural plant communities are frequently observed to have spatial structure, while some experiments demonstrate that spatial structure affects the intensity and outcome of interspecific interactions (Mack and Harper, 1977; Pacala, 1997; Stoll and Prati, 2001). These results confirm a longstanding perception that plants respond to their immediate neighbours rather than overall densities (Harper, 1977; Gibson et al., 1999).

Several researchers have used hexagonal lattices to control the neighbourhoods of plants, especially in multispecies plant competition experiments (Harper, 1977; van Andel and Dueck, 1982; Thórhallsdóttir, 1990; Milbau et al., 2003). A hexagonal lattice has simple neighbourhoods, in which the relative positions of the six neighbours of each plant are equivalent (Milbau et al., 2003). This can also be important when studying animals interacting with plants, such as pollinating bees (Cartar and Real, 1997). A hexagon also provides more boundaries across which species can interact than a square (Thórhallsdóttir, 1990). In rectangular arrays diagonal neighbours can intrude upon the interface between orthogonal neighbours (Barthram et al., 2002). Conversely, it is difficult to maintain equivalence among diagonal interactions in a rectangular grid. As a planting develops, some diagonal interactions may be blocked by orthogonal neighbours, while others converge to become like orthogonal interactions. Therefore the impact of competition from different diagonal and orthogonal neighbours may be difficult to predict or determine.

A variation is the hexagonal fan experiment, which allows analysis of the effects of plant density on interspecific interactions (Antonovics and Fowler, 1985; Schmid and Harper, 1985). In these experiments, a hexagonal lattice planting arrangement is expanded away from the apex of a triangle or the centre of a circle, so that the spacing between plants is increased by a set proportion for each successive row or arc. Despite difficulties with their statistical analysis, these designs revealed strong density-dependence in interspe-

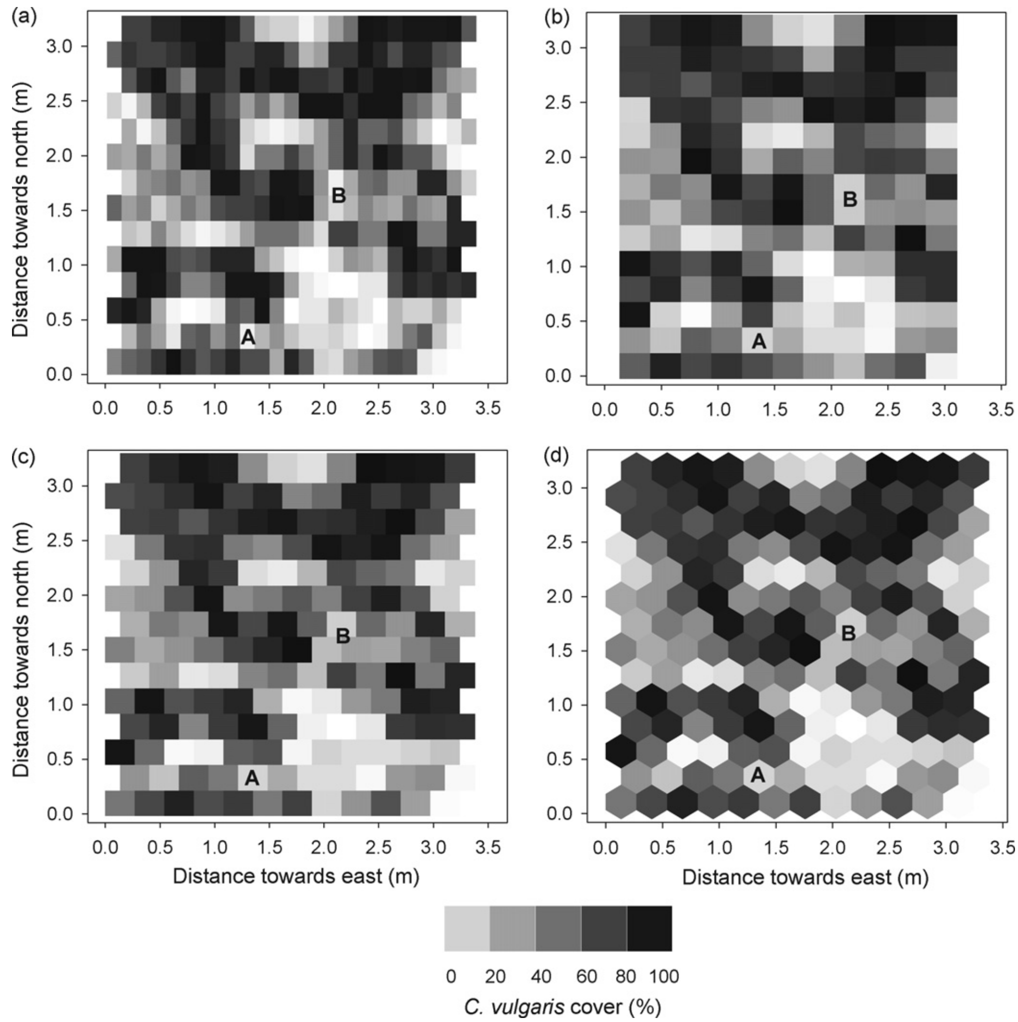

Fig. 2 – Grid-based maps of observed *Calluna vulgaris* (L.) Hull cover at a montane heath field site in the Scottish Highlands. Shading indicates the cover of *C. vulgaris*, being darkest for 100% cover. All four maps visualize the same information. (a) A full presentation of the observations as a rectangular grid of oblongs 23.2 cm × 13.4 cm. (b) Pairs of oblongs from (a) combined to form a rectangular grid of oblongs 23.2 cm × 26.9 cm. (c) Pairs of oblongs from (a) combined to form a hexagonal lattice of oblongs 23.2 cm × 26.9 cm. (d) The same map as (c), but with oblongs replaced by hexagons with equal area. The labels A and B indicate points referred to in the text.

cific interactions (Antonovics and Fowler, 1985; Schmid and Harper, 1985; Gibson et al., 1999). Equivalent results would have required many times more resources using treatments with fixed planting densities (Antonovics and Fowler, 1985).

5. Modelling

5.1. *Nearest neighbourhood and paths of movement*

For modelling, an important advantage of the hexagonal grid is the unambiguous definition of nearest neighbourhood: each hexagon has six adjacent hexagons in symmetrically equivalent positions (Birch et al., 2000). In contrast, the rectangular grid has two different kinds of nearest neighbour: orthogonal neighbours sharing an edge and diagonal neighbours sharing only a corner. The four neighbourhood including only the four orthogonal neighbours of each cell, sometimes called the "von Neumann neighbourhood", is incomplete, because the vertices of the tessellation are treated as empty barriers. The eight neighbourhood additionally including diagonal neighbours, sometimes called the "Moore neighbourhood", introduces complications related to the differences between the two kinds of nearest neighbour (Childress et al., 1996). The four and eight neighbourhoods are the opposite extremes of a spectrum of relative weightings for diagonal interactions versus orthogonal interactions (Birch, 2006). Simulations on rectangular grids require a setting for the relative weighting of diagonal interactions, which is avoided by using a hexagonal grid (Schumaker, 1996; Kreft et al., 1998; Birch, 2006). However, if sufficient information about spatial processes is available, this additional flexibility of the rectangular grid can be an advantage.

Whether or not adjacent cells should affect each other's interactions may determine the definition of nearest neighbourhood. Military simulations often emphasize this issue

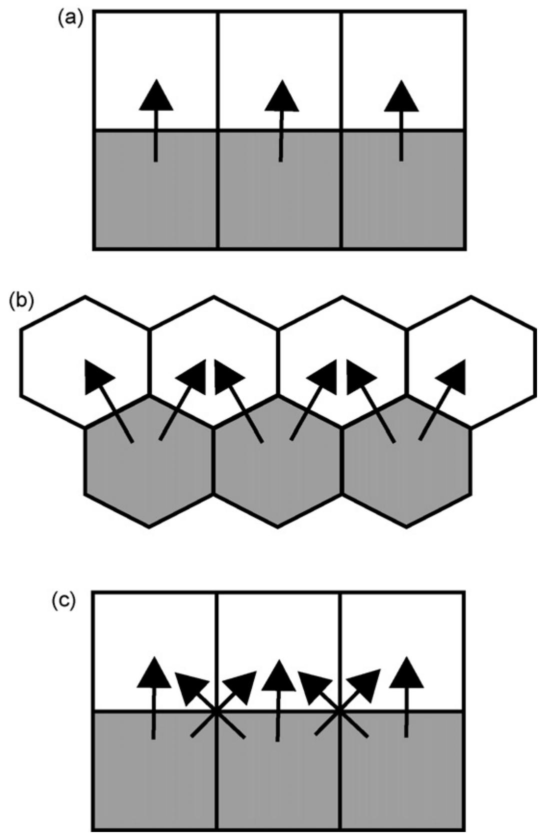

Fig. 3 – Potential nearest neighbour interactions at a boundary in a grid-based simulation. (a) With a four cell neighbourhood including only orthogonal neighbours, interactions are limited to pairs of cells. (b) In a hexagonal grid interactions are affected by neighbours. (c) With a eight cell neighbourhood including diagonal and orthogonal neighbours, interactions are affected by neighbours on both sides.

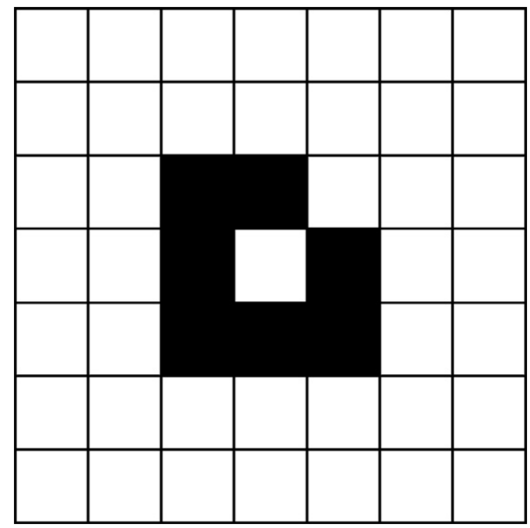

Fig. 4 – A well-known paradox resulting from neighbourhood definitions in rectangular grids. If only orthogonal links are accepted, the black cells form a broken ring that encloses the central white cell. If diagonal and orthogonal links are accepted, the black cells form a complete ring, but the central white cell is not enclosed!

(Palmer, 1977), but it seems to have been neglected in biology (Birch, 2006). Consider the front of a spreading area of occupation (Fig. 3). If a model is simulating a diffusion process, in which each cell contains many individuals moving distances that decline to zero as the time step is reduced to zero, the spread from adjacent cells should not interact. Therefore the four neighbourhood is most appropriate, so each invaded cell is invaded from a single occupied cell (Fig. 3a). Hence simulations with four neighbourhoods tend to have dynamics in which a single isolated cell can propagate whenever any larger group of cells can propagate (Birch, 2006). In contrast, many biological processes have ranges independent of the length of a time step. For example, dispersal often involves long movements during intervals that are very short relative to organisms' life spans, or translocation along a plant stem or stolon is very rapid compared to the rate of plant growth. In simulations of these processes, the influences from adjacent cells may interact. For example, the probability of successful invasion into a new cell may increase with the number of occupied cells contributing. A hexagonal grid, or non-zero diagonal interactions in a rectangular grid can allow such local interactions (Fig. 3b and c) (Birch et al., 2000; Birch, 2006).

The path of movement through a grid depends on the nearest neighbourhood, which defines the acceptable sequences of movements (Liu et al., 1995; Schumaker, 1996; Anneville et al., 1998). Within rectangular grids, there is a well-known inconsistency between the representation of movement and barriers (Fig. 4) (Rosenfeld, 1970). When movement is restricted to orthogonal steps, it can be blocked by barriers that include diagonal links. Yet, when movement can include diagonal steps, it can only be blocked by barriers consisting entirely of orthogonal links. This paradox can be resolved by proposing that diagonal movement implies a process with finite range, which can span a narrow barrier (Fig. 4). Mapping on to a rectangular grid can create related ambiguities, because diagonally neighbouring cells of matching habitat can be parts of a single habitat patch or from two separate patches (Fig. 2). These problems have encouraged the use of hexagonal grids to study the impacts of partial habitat destruction and for representing habitat patches from maps when connectivity is considered important (Liu et al., 1995; Tilman et al., 1997b). However, connectivity indices are frequently calculated from rectangular grids without comment, which may be inadvisable (McNeil et al., 2006; Ray and Burgman, 2006).

5.2. *Radial distance and isotropy*

Often simulations refer to the neighbourhoods of foci, beyond their nearest neighbourhoods, but still close relative to the full area represented (Weiner and Conte, 1981; Perry and Gonzalez-Andujar, 1993; Tilman et al., 1997a). This leads to a dilemma: should distance be defined in terms of Euclidean geometry in actual space (straight line distance), or in terms of the model's grid? For example, representations of plant dispersal have often used Euclidean distances (Table 2) (Clark, 1998;

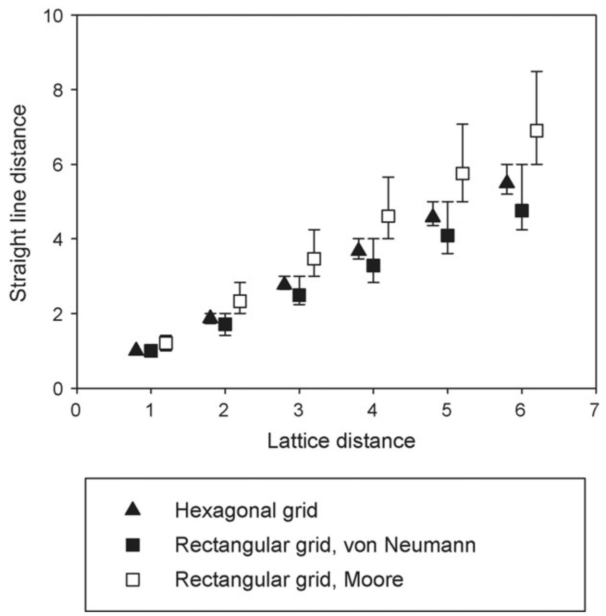

Fig. 5 – Relationship between straight line distance and grid distance. Points indicate straight line distance for grid distances up to 6, averaged over direction. Ranges indicate the maximum and minimum straight line distances for given grid distance.

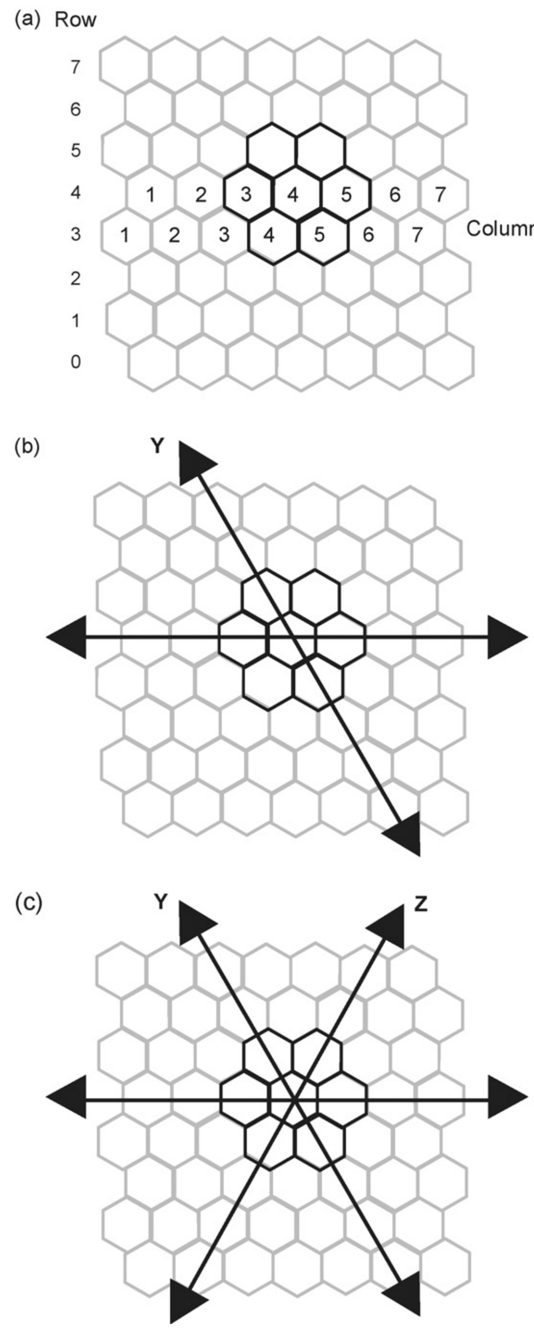

Fig. 6 – Three alternative co-ordinate systems for a hexagonal grid. (a) A row and column co-ordinate system. (b) A bidirectional, two row co-ordinate system. (c) The three row system used for the Symmetrical Hexagonal Co-ordinate System (SHCS).

Hovestadt et al., 2001), while models of plant resource uptake often use grid-based distances, sometimes called 'Manhattan distances' (Grist, 1999; Pachepsky et al., 2001). This dilemma will be less severe if the mapping between the two measures is consistent. The ratio of grid distance to Euclidean distance varies less with direction in the hexagonal grid than in the rectangular grid. The hexagonal grid is sometimes described as more isotropic than the rectangular grid for this reason (Anneville et al., 1998). The Euclidean distances for any given grid-based distance have half the range on a hexagonal grid as on a rectangular grid (Fig. 5). Hence successive grid distances represent discrete ranges of Euclidean distance up to a grid distance of seven cells on a hexagonal grid, but only up to three cells on a rectangular grid. Using a hexagonal grid may avoid the need to distinguish Euclidean and lattice distances, which has complicated the application of some simulations on rectangular grids (Perry and Gonzalez-Andujar, 1993; Tilman et al., 1997a; Hovestadt et al., 2001).

5.3. *Co-ordinates and orthogonality*

Probably the decisive reason for the dominance of rectangular grids in biological modelling is their symmetric cartesian co-ordinates on orthogonal axes. Orthogonality allows movement parallel to the two axes to be treated as independent, while symmetry allows the axes to be treated as interchangeable. These properties make the rectangular grid strongly preferred for models calculated by partial differential equations. No hexagonal co-ordinate system matches both of these properties.

There are three main alternative co-ordinate systems for hexagonal grids. The irregular rectangular co-ordinate system, with the two co-ordinates row number and position in row (Fig. 6a), may be the simplest way to label hexagons. Because the axes are orthogonal, it is easy to convert to absolute *x*–*y* co-ordinates for visualization, and the approximate relationship to a rectangular grid is intuitive. However, two asymmetries undermine this co-ordinate system: spacing differs along the two axes, and alternate rows are offset. These irregularities complicate the development and programming of simulations and increase the risk of errors. An alternative co-ordinate system defines axes along two rows (Fig. 6b). This system has equal spacing along the two axes, and no offsets. However, the axes are not orthogonal and the system is not symmetrical with regard to angular transformations, which complicates the representation of rotations or changes of direction.

A more consistent framework is the Symmetrical Hexagonal Co-ordinate System (SHCS) (Her, 1993, 1995). In this system three axes cross in the origin hexagon, at 60° to each other, along the three rows of hexagons (Fig. 6c). Because this system is symmetrical, measurements of distance are the same in all orientations, and rotation matrices can be defined. Her (1993, 1995) describes the calculation of distance and simple transformations in his two papers. However, this system is not orthogonal, so that any transformation along one axis will affect two co-ordinates. There is a built in redundancy in using triple co-ordinates (x, y, z) for points in a plane, which SHCS conventionally defines as:

$$\forall(x, y, z) : x + y + z = 0 \tag{1}$$

This redundancy can be useful for checking data capture of co-ordinates through a simple checksum mechanism.

The irregular rectangular system may be adequate for visualization, data capture and analyses that do not involve spatial relationships. However, when spatial relationships are considered, including vegetation dynamics and animal movement studies, the SHCS is preferable, because of its mathematical consistency and convenience. For example, the Euclidean distance between the centres of two hexagons can be calculated using the formula:

$$D_{\text{Eucl.}}[(x_1, y_1, x_1), (x_2, y_2, x_2)] = \sqrt{\tfrac{1}{2}[(x_1 - x_2)^2 + (y_1 - y_2)^2 + (z_1 - z_2)^2]} \tag{2}$$

where (x_1, y_1, z_1) and (x_2, y_2, z_2) are the co-ordinates of the two hexagons. Alternatively, the distance in number of grid cells is:

$$D_{\text{Grid}}[(x_1, y_1, x_1), (x_2, y_2, x_2)] = \max(|x_1 - x_2|, |y_1 - y_2|, |z_1 - z_2|) \tag{3}$$

6. Hierarchical grids

There is increasing awareness that biological spatial patterns are dependent on the spatial resolution at which they are observed (Kotliar and Wiens, 1990; Wu and Loucks, 1995; Fauchald, 1999; Lennon et al., 2001). Related research may modify the resolution of a simulation or map by composing cells into larger cells, or decomposing them into smaller cells (Lennon et al., 2001). Combining multiple grid scales within a simulation also assists the combination of individual-based models with grid-based environments (Beecham and Farnsworth, 1998). Alternatively, users may want to smooth or simplify a grid by reducing its resolution. Composition and decomposition of squares in a rectangular grid is straightforward and maintains congruency and alignment. In other words, each square at a coarse scale is composed of an integer number of entire squares at a finer scale, every cell point matches a cell point at a finer scale, and axes remain the same for all scales (Sahr et al., 2003). In contrast, a hexagon cannot be composed of entire smaller hexagons. Hexagonal grids have been composed or decomposed using two types of method: the use of partial hexagons, and non-hexagonal composition (Sahr et al., 2003). Above we have already discussed a method of composition using oblongs which combines both of these approaches (Fig. 1).

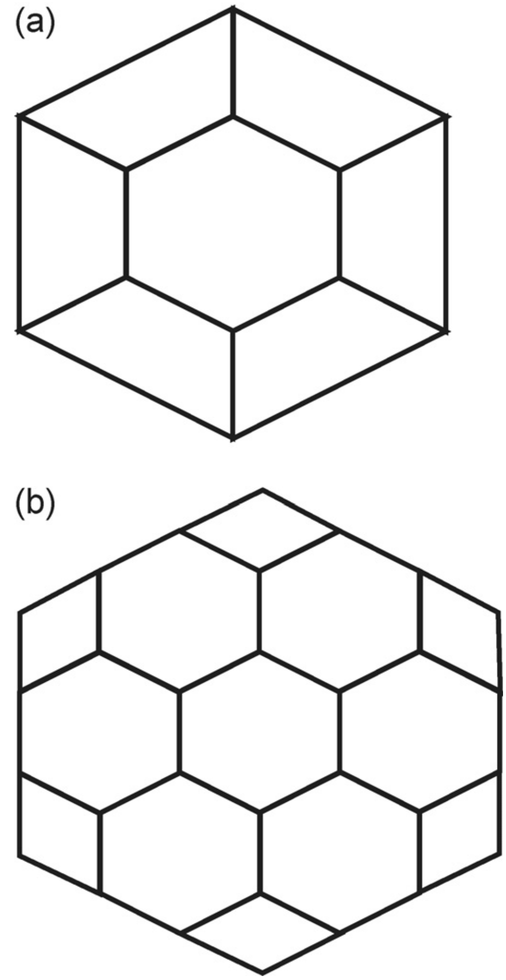

Fig. 7 – Incongruent, aligned decomposition of hexagons into (a) four and (b) nine partial hexagons, as recommended by White et al. (1992).

White et al. (1992) describe two schemata which use partial hexagons: one uses four hexagons (one whole and six halves), the other nine hexagons (seven whole and six thirds) (Fig. 7). It can be seen that the grids of each successive layer are exactly aligned. The global grid project uses the power four schema, dividing the world into $4^n + 12$ cells (12 are pentagons, to fold the hexagonal sheet close to an ellipsoid) (Sahr et al., 2003). These hierarchical schemata are ideal when there is no direct transfer of information between layers, for example when a Geographic Information System consists of layers with different resolutions derived from external data.

However, partial hexagons may not be acceptable for modelling animal movement and vegetation dynamics.

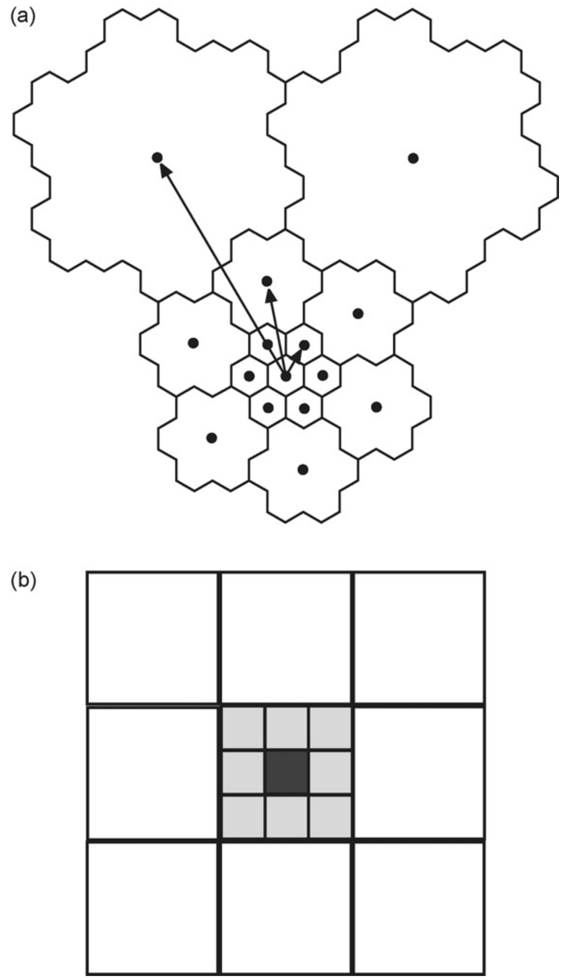

Fig. 8 – Congruent composition of (a) hexagons to form a Generalized Balanced Ternary, which is aligned but has different orientation at alternate levels of resolution, as indicated by the arrows between the centres of cells at different resolutions, and (b) squares to form an aligned rectangular grid. (a) was originally published in Oom et al. (2004).

An alternative is to group hexagons in sevens, which is appropriate for hierarchical modelling, because a nearest neighbourhood at the finer scale becomes a focal cell at a coarser scale (Fig. 8a) (Oom et al., 2004). These first order groups of seven ("heptads") also tessellate to form groups of seven first order patches and so on in any power of seven (Vince, 1993; Beecham and Farnsworth, 1998; Sheridan et al., 2000; Sahr et al., 2003). This hierarchy of tessellations has various names, including the Spiral Honeycomb Mosaic or General Balanced Ternary (Vince, 1993; Sheridan et al., 2000; Sahr et al., 2003). The analogous hierarchy in a rectangular grid uses a neighbourhood of nine squares to form a single larger square (Fig. 8b). Unfortunately a heptad of hexagons does not form a hexagon, nor does its tessellation maintain alignment, being rotated about 19° relative to the original hexagonal grid. The second order tessellation, containing 49 hexagons in each cell, can be aligned with the original hexagonal grid. Hierarchical co-ordinates are listed from highest order group down to individual hexagon, with the centre group or hexagon generally given a co-ordinate of zero (Beecham and Farnsworth, 1998; Sheridan et al., 2000).

7. Discussion

There appear to be strong qualitative contrasts between rectangular and hexagonal grids. The rectangular grid has a symmetric, orthogonal co-ordinate system, simplifying calculations and transformations on the grid. It is also convenient for studies varying resolution, such as hierarchical grids, because squares can easily be combined to form larger squares with the same alignment. However, the survey in this paper revealed very few applications of hierarchical grids, despite attempts to combine continuous individual-based models with grid-based environments (e.g. Morales et al., 2006; Parry et al., 2006; Reineking et al., 2006), which is the classic application for hierarchical grids (Beecham and Farnsworth, 1998). The four neighbourhood is the only grid system with interactions restricted to being purely between pairs of cells (Fig. 3, Birch, 2006), and it is almost by definition the system for calculations with partial differential equations.

On the other hand, the hexagonal grid has a simpler and more symmetric nearest neighbourhood, which avoids the ambiguities of the rectangular grid. The rectangular grid's inconsistencies are especially likely to undermine studies of connectivity (Fig. 4) (Rosenfeld, 1970). The calculation of least cost distance may be the application in Table 2 most likely to benefit from changing from a rectangular grid to a hexagonal grid (McNeil et al., 2006; Ray and Burgman, 2006). The hexagonal grid also provides a substantially better match between distances measured in grid units and straight line (Euclidean) distances, which might make a coarse hexagonal grid more acceptable for modelling dispersal than a coarse rectangular grid (Table 2). Another advantage of the hexagonal grid is its greater clarity when used for visualization (Fig. 2) (Carr et al., 1992). Other differences between the two grids seem relatively minor.

Authors have mentioned the relatively trivial advantages of the hexagonal grid for precise sampling more often than its advantages in visualization (Overton et al., 1990). However, the visual advantages are probably the main reason for the hexagonal grid's early adoption in recreational military simulations (Palmer, 1977; Dunnigan, 1992). There may well be scope for greater use of the hexagonal grid specifically for visualization (Carr et al., 1992). Self-organizing maps are an example of such an application (Gevrey et al., 2006; Park et al., 2006). A model or map could be run or prepared using a rectangular grid, but visualized as a hexagonal grid (e.g. Fig. 2).

The difficulties associated with hexagonal co-ordinates and composition and decomposition of hexagonal grids can be overcome (Her, 1993, 1995; Beecham and Farnsworth, 1998; Sahr et al., 2003). Here we have demonstrated that using or generating a hexagonal lattice in field survey is straightforward. Currently GIS rasters in ecology are almost always rectangular grids. However, there is no intrinsic reason why they cannot be hexagonal grids. In principle remotely sensed images can just as well be rectified to hexagonal grids as rectangular grids. Therefore the hexagonal grid should be preferred when it has advantages for the construction or representation of nearest neighbourhood, movement or connectivity. Visualization as a rectangular grid map may also be undesirable. However, when the differences between the grids are minor, the rectangular grid may be more convenient. Moreover, the specific properties of the rectangular grid may be useful, such as the contrasts between orthogonal and diagonal nearest neighbour interactions (Birch, 2006). The selection of an appropriate grid should be based on the requirements and objectives of the application. The reasons for using a particular grid should be made clear in the methods sections of related publications.

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