18th World IMACS / MODSIM Congress, Cairns, Australia 13-17 July 2009
http://mssanz.org.au/modsim09

Modelling Spatial Substructure in Wildlife Populations using an Approximation to the Shortest Path Voronoi Diagram

Stewart, C.W.[1,2] **and R. van der Ree**[1]

[1] *Australian Research Centre for Urban Ecology*
[2] *University of Melbourne*
Email: c.stewart9@pgrad.unimelb.edu.au

Abstract: In the field of conservation biology, accurate population models are important for managing wildlife. It has been acknowledged that spatial structure should form an integral part of such models. Advancement in the power of desktop computers has allowed biologists to construct individual-based, spatially-explicit simulation models to predict the population dynamics of species. These models take into account local interactions and output emergent trends. However, whilst in many cases such models have been useful, for large landscapes, they may still be too computationally expensive. An alternative approach is to construct a metapopulation model. These are usually less computationally expensive, and whilst they often incorporate less detail than spatially-explicit models, they may still include enough spatial structure to be ecologically realistic. However, the assumption made in metapopulation models, that any individual within a patch can interact with any other individual of the patch may not always be appropriate. For example, in social species where the size of the social group home range is much smaller than the average patch size, individuals in a social group from one part of the patch may not interact with individuals from another social group in another part the patch. In such cases it is useful to consider spatial structure within the patch itself.

In this paper we propose using the Shortest Path Voronoi Diagram (SPVD) to model the spatial structure within patches for social species. For such a diagram we use seeds to represent the centres of the social groups in each patch. We then assign each point of the patch to the seed it is closest to (where distance is measured with the shortest path metric). This partitions each patch containing seeds into regions. Together these regions form the SPVD. By linking the seeds of neighbouring Voronoi regions with shortest paths, a network among social groups is created. This can be used to model the dispersal paths of a population.

Whilst analytic algorithms exist for the construction of the SPVD, these have often been developed for a polygonal domain. In complex landscapes, the time-complexity of such algorithms may become just as slow as grid-based approximations. Moreover, analytic methods may be less numerically robust and harder to extend to more complex variations of the Voronoi diagram. In this paper we offer a new grid-based approximation for the shortest path Voronoi diagram referred to as the quadtree-grid Voronoi Diagram (or q-grid VD). The construction procedure involves a decomposition of the landscape into a quadtree, and a propagation of circular wavefronts from each seed through a grid that is laid over the quadtree structure. We show how the q-grid VD can be applied to a wildlife population model using a squirrel glider (*Petaurus norfolcensis*) population in a semi-rural landscape as an example. By averaging outputs across multiple q-grid VDs we generate a time series of density maps. Such maps could be useful for informing wildlife management.

Keywords: *Shortest Path Voronoi Diagram, quadtree, q-grid Voronoi Diagram, population model*

1. INTRODUCTION

Metapopulation models have been useful in many applications for modelling population dynamics in a spatial setting (Hanski 1998). However, they often do not account for the effects of spatial structure within the patch itself. Spatial models have been developed for continuous habitat, but often in a theoretical setting without any consideration for the geometry of the patch (Law *et al*. 2000); furthermore, they are computationally expensive and therefore impractical for use with large landscapes. In this paper we present a new method for modelling the spatial substructure of wildlife populations. The method is targeted at social species that form social groups with home ranges much smaller than patch size. The development of our method grew out of a practical need for a way to model the population dynamics of the squirrel glider. We decided that the traditional metapopulation framework would be unsuitable for this species as patches were too large to ignore the effects of space within them; moreover, we decided that other more spatially-explicit models would demand too much computer memory and would be too slow given the extent and resolution of the landscapes we wished to consider. The method we developed, models within-patch spatial structure with a new type of Voronoi diagram that we refer to as the q-grid VD; this approximates the SPVD. The q-grid VD is inspired by grid-based methods for finding shortest paths in the robotics literature. Chen *et al*. (1997) use "wave" propagation (discussed in section 3) through a modified quadtree (a data structure discussed in Section 2) to find shortest-paths. Our algorithm propagates multiple waves simultaneously through a q-grid from multiple seeds to construct a q-grid VD. In this paper we introduce the q-grid VD with a procedure for its construction and then show how it can be applied to a population model.

2. CONCEPTS

A quadtree is a type of tree data structure that can be constructed from a $2^n \times 2^n$ binary input array. Its nodes are coloured *gray*, *black*, or *white*. Every quadtree has at least one node called the *root* node. The root's colour is determined by the values in the whole input array. If the input array has values that are all 0 or all 1, then the root's colour is white or black, respectively, and the quadtree has no more nodes. If, however, the input array has values of both 0 and 1, then the root is coloured gray and is linked to four child nodes. These child nodes are labeled and ordered *north-west child*, *north-east child*, *south-west child* and *south-east child*, and their colours are determined in a similar way by sub-arrays $[0{:}2^{n-1}{-}1]\times[0{:}2^{n-1}{-}1]$, $[2^{n-1}{:}2^{n}{-}1]\times[0{:}2^{n-1}{-}1]$, $[0{:}2^{n-1}{-}1]\times[2^{n-1}{:}2^{n}{-}1]$ and $[2^{n-1}{:}2^{n}{-}1]\times[2^{n-1}{:}2^{n}{-}1]$ respectively of the input array. If any of these children are gray then they are themselves linked to four children whose colours are determined similarly by another group of four subarrays, and so on. (Note: we follow the convention of writing the column coordinate before the row coordinate. Furthermore, for points in the plane, we set the *y*-axis in a clockwise-perpendicular direction from the *x*-axis. Both these conventions are followed so that columns and rows easily match up with *x* and *y* coordinates.) Gray nodes are referred to as the *parent* of their children and black and white nodes are called *leaf nodes* or *quads*. Figure 1(a) shows a binary input array and Figure 1(b) the resulting quadtree. Gray nodes are drawn with open circles, white nodes with open squares and black nodes with filled in squares. For each quadtree there is a unique input array of smallest dimensions from which it can be constructed. We call this array the *quadtree array*. Furthermore, we call each subarray of the quadtree array that corresponds to a quad, a *quad array*. The quadtree array for the quadtree in Figure 1(b) is identical to the array in Figure 1(a). In Figure 1(b), links between child and parent nodes are drawn with straight-line segments. The children of a parent form part of the row of nodes below the parent and they are drawn from left to right in the child order given above.

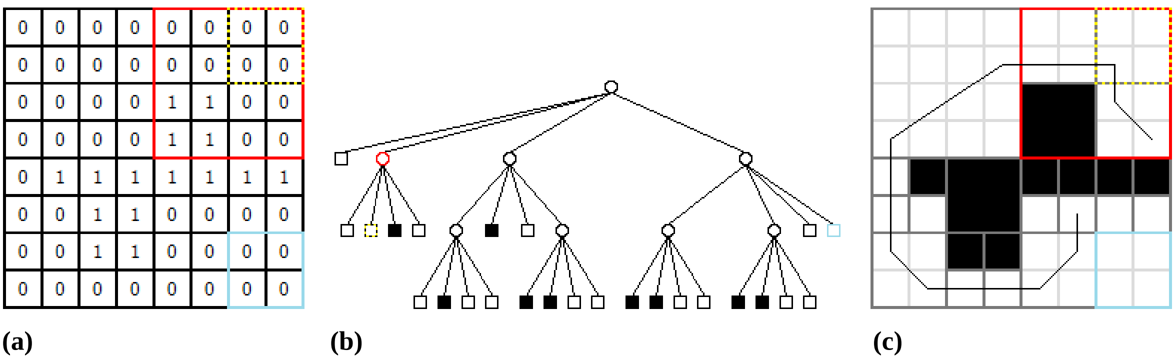


Figure 1. (a) A $2^3 \times 2^3$ binary input array; (b) the resulting quadtree; (c) and the corresponding planar representation with the image of a q-grid shortest path on Q_0. The colours indicate corresponding features. We label the red subarray in (a), red node in (b) and red planar representation in (c): R_a, R, and R_p respectively. We label the yellow and blue features similarly: Y_a, Y, Y_p, B_a, B, B_p. In (b), circles, open squares and filled in squares represent gray, white and black nodes respectively.

We will now look at three of the nodes in Figure 1(b). Since the input array (Figure 1(a)) has values of both 0 and 1, the root, drawn at the top of Figure 1(b), is gray and is linked to four children. Its north-east child, R, is determined by the values in the subarray R_a. Since this subarray has values of both 0 and 1, the node R, is gray and is linked to four children. Its north-east child, Y, is determined by the values in the subarray Y_a. Since this subarray consists entirely of values of 0, the node Y is white, has no children and is called a leaf node or quad. We call Y_a the quad array corresponding to Y.

If we think of the columns and rows of a quadtree array, A, as integer x and y coordinates in the plane, then we can think of the quadtree as representing the set $[-1/2,2^n-1/2]^2 \subseteq \mathbb{R}^2$. Each node then has a square planar representation. For example, quad B in Figure 1(b), has the square planar representation of B_p in Figure 1(c). We call the square planar representation of a node, a *quad square*, if the node is a quad. We call the union of all white quad squares (including their boundaries) the *white space* and label it W. Furthermore, we call the union of the boundaries of all quads (white and black) the *quad lines*. In Figure 1(c) black and white quad squares are coloured accordingly and quad lines are drawn with bold dark gray lines and bold red, blue and yellow coloured lines. Since there is a correspondence between subarrays, nodes and planar representations, the term *quad* can be used loosely to describe a quad array, a leaf node, or a quad square depending on the context. For example, in Figure 1, B_a, B, and B_p are all essentially the same "quad". We say two points $x, y \in W$ are *quad connected* if they are either in the same quad or if there is a sequence of quads $S_1,\ldots,S_m$ such that $x \in S_1$, $y \in S_m$ and the boundary of S_i intersects with that of S_{i-1} at some points other than corner points. In Figure 1(c), any point in Y_p is quad connected to any point in B_p. We define the function $\psi : W \to \{0,1\}$ by $\psi(x,y)=1$ if x and y are quad connected and $\psi(x,y)=0$ otherwise. A quadtree grid (or q-grid) Q_i is a finite arrangement of points defined only on the white space. The q-grid Q_0 is called the *base grid* and consists of points in the plane with integer coordinates corresponding to the zero values in the quadtree array. For $i \ge 1$, Q_i is finer than Q_{i-1}; to construct Q_i each point in Q_{i-1} is replaced by four new points that form the corners of a square of width $1/2^i$ centred on the point being replaced. Thus, we define a *q-grid* Q_i, with a grid interval of $1/2^i$, by $Q_0 = \mathbb{Z}^2 \cap W$ when $i = 0$, and when $i \ge 1$, by $Q_i = \left\{ \left(x + \sum_{k=1}^{i} v_k / 2^{k+1}, y + \sum_{k=1}^{i} w_k / 2^{k+1} \right) : x, y \in Q_0 \text{ and } v_k, w_k \in \{-1,1\} \right\}$. Each point (a,b) in Q_i has a planar region associated with it, namely $[-1/2^{i+1}+a, 1/2^{i+1}+a] \times [-1/2^{i+1}+b, 1/2^{i+1}+b]$. We use the term *q-grid cell* loosely to refer to both $x \in Q_i$ and its planar region. The union of all boundaries of all such planar regions for a q-grid Q_i constitutes the *q-grid lines* of that q-grid. In Figure 1(c), the q-grid lines of Q_0 are drawn with bold light gray lines. (Note that some are hidden under the quad lines.)

We define a (general) path in W to be a continuous function $\gamma : [0,1] \to W$. Without giving a precise definition we will let $L(\gamma)$ denote its length. We say (a general path) γ is a *shortest path* if $L(\gamma) = \inf \{ L(\sigma) : \sigma \in P \}$ where P is the set of all paths from $\gamma(0)$ to $\gamma(1)$ in W. (Note that in practice it is often satisfactory to think of a (general) path as the image of such a function.) A q-grid path is a particular type of path. We say that a path $\gamma : [0,1] \to W$ is a q-grid path on Q_i if $\gamma(0), \gamma(1) \in Q_i$ and if γ always enters and leaves quads along straight-line segments that run perpendicular to the quad lines they cross and which join adjacent q-grid cells from either quad. In Figure 1(c), the image of a q-grid shortest path between $(5,5) \in Q_0$ and $(7,3) \in Q_0$ is drawn with a black line.

We can now assign a q-grid distance between pairs of points in Q_i. Precisely, we define the function $d_i : Q_i^2 \to \mathbb{R}$ by $d_i(x,y) = \inf \{ L(\sigma) : \sigma \text{ is a q-grid path from } x \text{ to } y \text{ on } Q_i \}$ if $\psi(x,y)=1$ and $x \ne y$; $d_i(x,y)=0$ if $x = y$; and $d_i(x,y)=\infty$ if $\psi(x,y)=0$. It can be verified that Q_i together with d_i form a metric space and we therefore call d_i the q-grid metric. Let k distinct points $s_1,\ldots,s_k \in Q_i$ be called *seeds*, and let $S = \{s_1,\ldots,s_k\}$ be called the *seed set*; we define the *q-grid Voronoi set* associated with $s_m \in S$ to be all those points in Q_i closer to s_m (in the q-grid metric) than to any other seed; that is, we define the set by:

$$V_i(s_m) = \{ p \in Q_i : \psi(p,s_m) = 1 \text{ and } d_i(p,s_m) \le d_i(p,s_n), \text{ for all } m \ne n, \text{ with } d_i(p,s_m) = d_i(p,s_n) \text{ only if } m < n \}$$

We define the *q-grid VD* to be the collection $\mathfrak{V}(S,d_i)=\{V_i(s_1),...,V_i(s_k)\}$. For any $x\in W$ we define $\beta_i(x)$ to be any element from Q_i that is closest to *x*; so $\beta_i(x)$ is defined to be any element from the set $\{z\in Q_i : \|x-z\|\le\|x-w\| \text{ for all } w\in Q_i\}$. Now each q-grid Voronoi set $V_i(s_m)$ has a planar representation consisting of the union of all the planar representations of the q-grid cells in Q_i. The planar representation of $V_i(s_m)$ is $E_i(s_m)$ where the set $E_i(g)$ is defined for any $g\in W$ to be:
$\{(u,v)\in W : \max\{|u-x|,|v-y|\}\le 1/2^{i+1} \text{ for some } (x,y)\in V_i(\beta_i(g))\}$. Figure 2(a) shows the planar representation of the q-grid Voronoi diagram on Q_0; 2(b) on Q_2; and 2(c) on Q_6. The black filled in circles represent seeds. The coloured regions represent the sets $E_i(s_m)$. Note that in this figure the quadtree remains fixed, but the planar representations of the q-grid Voronoi sets change as the q-grid get finer; recall also that each q-grid Q_i is defined only in the white space. (Figure 2 will be discussed further in Section 4.)

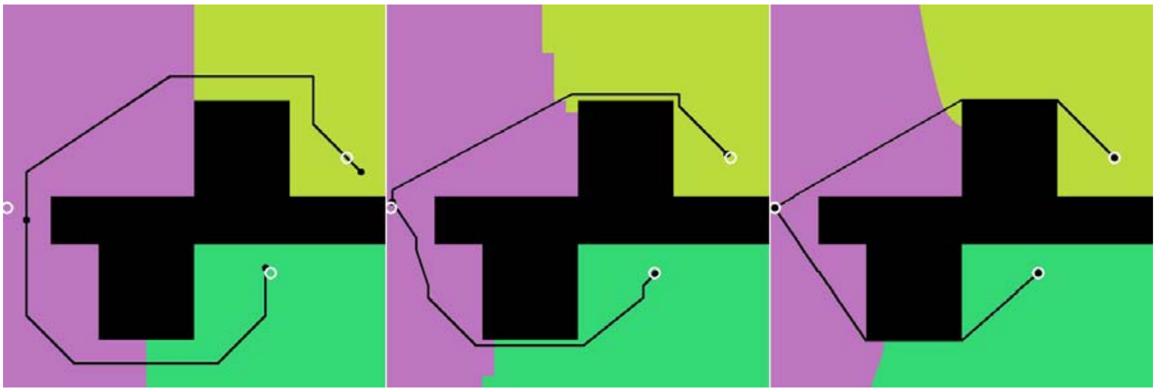
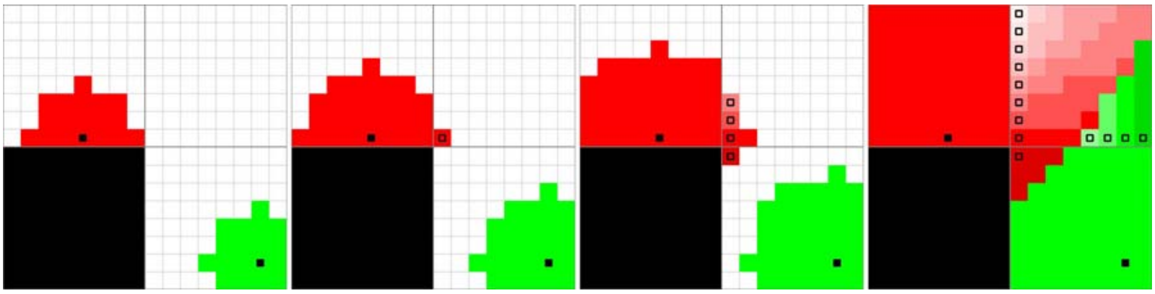


Figure 2. Planar representations of a q-grid VD (a) on Q_0; (b) on Q_2; (c) on Q_6. Open white circles show target seed positions and the black filled in circles the q-grid seed positions. The coloured regions are the planar representations of the q-grid Voronoi sets. Black seeds are linked by q-grid shortest paths.

3. THE ALGORITHM

We give a brief overview of the core procedure in our algorithm by using the example illustrated in Figure 3. In our algorithm the cells of a q-grid Q_i act as data structures each with many fields; here we consider only the fields called *global_id*, *id*, and *dt* (which stands for distance transform). The algorithm assigns values to the cells in discrete time at unit intervals. This process, referred to as propagation, happens in a wave-like manner through the q-grid Q_i. When a cell has been assigned values it is said to be covered. To start with, the seeds with which we associate our Voronoi sets are covered. We refer to these seeds here as zero-seeds. They are each covered with a global_id value that is unique amongst seeds across the q-grid, an id value that is unique amongst seeds in the same quad, and a dt value of zero. Zero seeds are shown in Figure 3 as small black filled in squares. After this initialisation, the uncovered cells in each active quad containing zero seeds are covered iteratively; at time $t > 0$, cells that are at a Euclidean distance *d* from a zero seed, such that $t-1<d\le t$, are covered. They are assigned the same global_id as the zero seed and a dt equal to *d*; we say that the zero seed has covered these cells. In Figure 3(a) the state of the quadtree is shown after three time iterations. When a border cell is covered, we prepare any adjacent uncovered cell it may have in an adjacent quad to be an entry point for the wave into that quad. To do this we use a function that searches for a neighbouring quad using the links of the quadtree structure. In Figure 3(a) the border cell at *f*(7,7) (where f:{0,...,15} × {0,...,15}→Q_3 is defined by $f(x,y)=(x/8-7/16,y/8-7/16)$) has just been covered and so its neighbour at *f*(8,7) is prepared as an entry. During the next iteration this cell is covered and its quad becomes active; the cell is assigned: a dt equal to the dt at *f*(7,7) plus one, the same global_id as *f*(7,7), and an id unique amongst the seeds in the quad. Once covered it is called a time-seed. In Figure 3(b) *f*(8,7) is shown as a covered time-seed. A time-seed *x* can cover cells in its quad at time $t > 1$ that are at an Euclidean distance *d* from it, such that $t-1<d+\mathrm{dt}[x]\le t$ (where dt[*x*] denotes the distance transform value at cell *x*). Such cells are assigned a dt equal to dt[*x*]+*d*, and a global_id the same as *x*. If multiple cells are trying to cover a cell *y*, then *y* is covered by the competitor cell that can cover it with the smallest dt value. If multiple competitors can achieve this, then *y* is covered by the competitor with the lowest global_id. This process of propagating values through the q-grid Q_i, marks out the Voronoi sets. In Figure 3(d) the red cells belong to

the Voronoi set associated with the seed at $f(4,7)$ and the green cells belong to the Voronoi set associated with the seed at $f(14,14)$.



(a) **(b)** **(c)** **(d)**

Figure 3. Propagation on Q_3 at time 3, 4, 5 and 14 is shown in (a), (b), (c) and (d) respectively. Small filled in black squares represent zero seeds, while time seeds are open. Shades of red distinguish between the regions covered by the different red seeds; similarly for the shades of green.

4. APROXIMATION

In this section we state a Theorem and a Corollary that express the approximation properties of the q-grid VD. If W is the white space of a planar representation of a quadtree with a quadtree array of dimensions $2^n \times 2^n$, then $W \subseteq [-1/2,2^n-1/2]^2$ and $N=[-1/2,2^n-1/2]^2 \setminus W$ is an open set. Moreover, N will be a finite union of open, path-connected sets that have pair-wise empty intersections. (Each open set corresponds to the interior of a quad-connected region of black quads.) To simplify the situation we will assume that the pair-wise intersections of their closures are also empty. This assumption places the *constraint* on white quads that if any two white quads A and B share only a corner point in common on their boundaries, they must both be adjacent to another white quad C such that A and C share more than a corner and C and B share more than a corner. The following theorem can be proven.

Theorem

Let $x, y \in W$ such that $\psi(x,y)=1$ and suppose that the constraint on N (outlined above) is met; then $\lim_{i\to\infty} d_i\left(\beta_i(x),\beta_i(y)\right) = d_{\mathrm{sp}}(x,y)$ where d_{sp} is the true shortest path distance.

This fact can be observed in Figure 2. The open circles are centred on arbitrary points x in W. The black filled in circles represent the corresponding points in Q_i ; namely the points $\beta_i(x)$. We see that as i gets larger (moving from Figure 2(a) to 2(b) to 2(c)) the lengths of the q-grid shortest paths appear to approach a limit length. From this Theorem we conjecture that the following Corollary is true.

Corollary

Suppose that the constraint on N is met. Let $g_1,\ldots,g_k$ be distinct seeds in W, and let $V_{\mathrm{sp}}(g_m)$ be the shortest path Voronoi set associated with g_m; then for $g \in \{g_1,\ldots,g_k\}$ it follows that:

$$V_{\mathrm{sp}}(g) = \overline{\limsup_{i\to\infty} E_i(g)} = \overline{\liminf_{i\to\infty} E_i(g)} .$$

5. APPLICATION

We applied the q-grid VD to a population model for the squirrel glider (*Petaurus Norfolcensis*). The squirrel glider is a small aboreal marsupial native to Australia whose main form of locomotion is that of gliding from tree to tree (van der Ree 2003). It is rare for a squirrel glider to move along the ground and its glide length generally restricts its dispersal; therefore, the squirrel glider can be thought to perceive the landscape in a binary way, consisting of habitat and non-habitat. We used the q-grid VD in a stochastic simulation model for a glider

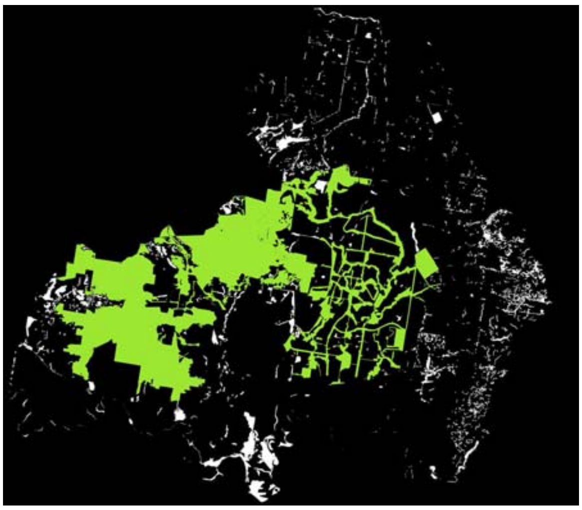
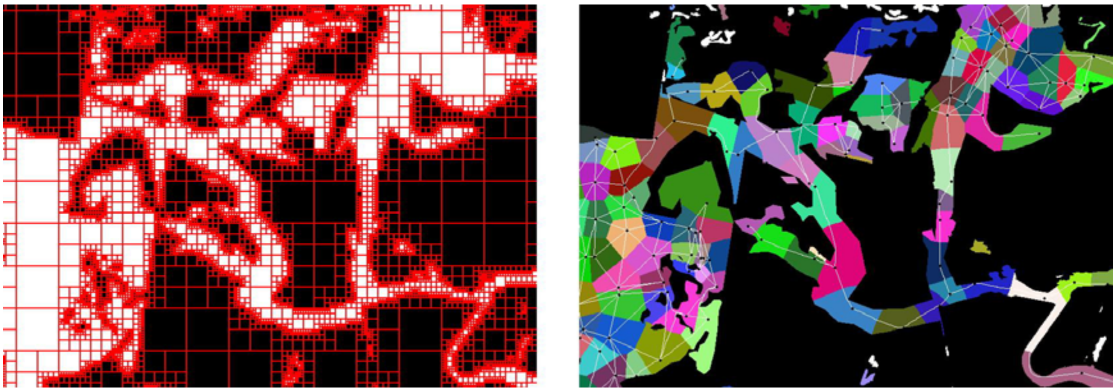


Figure 4. Vegetation map for the Albury Ranges and Thurgoona area in South Eastern Australia. (Green represents a connected focal patch, white all other patches, and black, non-habitat. North points to the top of the page)

population inhabiting a landscape with a large patch in the Albury Ranges and Thurgoona area of south-eastern Australia. The patch is green in Figure 4. It is approximately 5000 ha which is about 10^3 times larger than a typical social group home range size. We constructed a quadtree for the landscape using the method of Shaffer and Samet (1987). A close up of its planar representation is shown in Figure 5(a).



(a) (b)

Figure 5. (a) A close up of a quadtree planar representation and (b) a close up of a q-grid VD and its corresponding network for an arbitrary part of the landscape shown in Figure 4.

Once the quadtree was constructed we then assigned seeds to the q-grid Q_0. The seed positions were chosen randomly and the number of seeds used was determined by *K_density*Area/Ceiling*; where *K_density* is the density of animals permitted in the landscape at carrying capacity, *Area* is the total area of habitat in the landscape, and *Ceiling* is a parameter associated with social group size. Following this we constructed a q-grid VD using our algorithm and then a network by linking the seeds of neighbouring Voronoi sets in the q-grid VD with q-grid shortest paths following a similar procedure to Chen *et al*. (1997). The Voronoi sets and the resulting network were then used to represent social groups and dispersal routes, respectively, in a Population Dynamics Module (PDM). The PDM projected yearly glider numbers for each social group for 100 years. We ran the PDM 100 times and for each year averaged the numbers at each social group across the runs. For each social group and for selected years we then converted these numbers into densities, by dividing them by the area of the corresponding Voronoi sets (planar representations). These densities were stored in a q-grid type structure according to the positions of their Voronoi sets. We repeated this whole process 30 times with a different random assignment of seeds each time. By averaging corresponding grid cells we were able to produce densitiy maps for selected years. We choose to replicate the process 30 times as this smoothed out the variation in our spatial averaging. A close up of one of the q-grid VDs and its corresponding network is shown in Figure 5(b).

In the PDM, dispersal between social groups followed a random walk on the network. Juveniles dispersed after a year with distance given by an exponential distribution with a mean of 3km; after dispersing this distance they attempted to join the social group they reached. Dispersers that reached social groups that were at carrying capacity were made to die. Any male and female within a social group were permitted to breed if neither was a parent of the other, and if they were not full siblings. Successful breeding events between males and females produced a number of offspring based on a Poisson distribution with mean 2. Individual survival was determined by a set probability.

In Figure 6 we present some density map outputs from our model when an annual survival probability of 0.55 was used. The six maps shown have been cropped to focus on the central patch in the landscape. The figure shows population density declining until most of the landscape is close to a zero density at year 60. In another model run with a survival probability of 0.57, population density after 100 years varied across the landscape with some parts close to carrying capacity and other parts close to zero. For a survival of 0.6 most of the landscape was at carrying capacity after 100 years. We also looked at the effect of varying the Ceiling parameter in our model. We found that increasing this parameter (which decreases the number of seeds used) led to higher densities across the landscape at lower survivals. This suggests that accounting for less spatial structure in a population model than there actually is could lead to an overestimation in population viability. Our aim in this section, however, is not to give a detailed analysis of our results but to simply demonstrate that our method can be applied to a real landscape; it is intended that a more detailed analysis of our results will be described elsewhere.

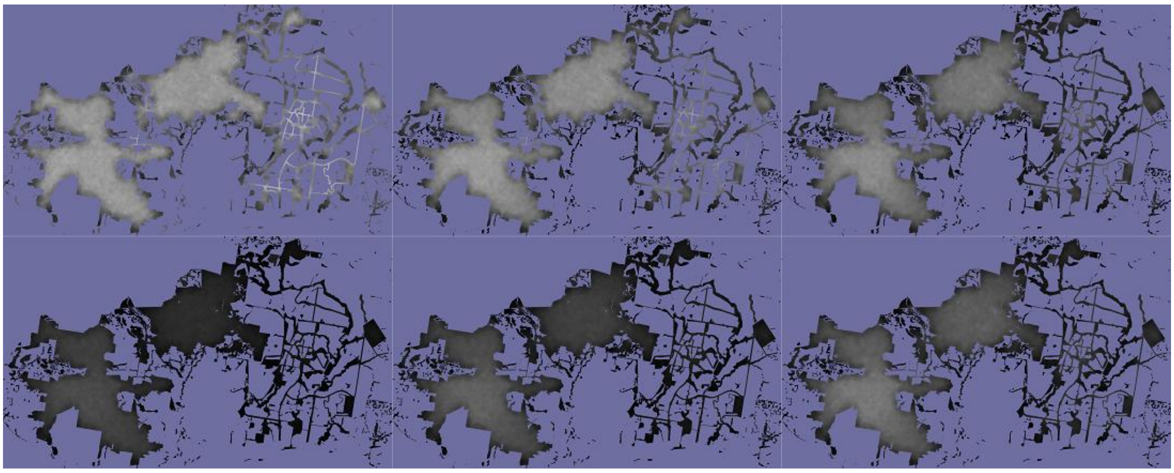


Figure 6. A time series of 6 density maps for the focal patch in Figure 4. Clockwise from top left, the maps show predicted squirrel glider densities for years 10 to 60 ahead in ten-year intervals. Each map represents model outputs averaged over 30 q-grid VDs with 100 population dynamics simulations averaged for each q-grid VD. The shades of gray indicate the density with white representing *K_density* and black a zero density.

6. FUTURE WORK AND CONCLUSION

There is a way to extend our model to landscapes with more categories than simply habitat and non-habitat. The different categories would have weights associated with them and the spatial structure would be modelled with a weighted q-grid VD. Szczerba *et al*. (1998) developed a path algorithm for such a setting. They used wave propagation, with waves travelling more slowly through quads with larger weights. In our extension, multiple waves from seeds would be propagated through a weighted q-grid. As before, the landscape would be distilled into a network linking social groups; but this time the links would have costs associated with them.

Whilst theoretical exact methods for SPVD construction have been described, the method described in this paper may be useful for the following reasons. Firstly, our method leads to grid-based outputs that are easily analysised in a computational setting. Secondly, it is likely that the extension to our model would have a better time complexity than exact methods; Szczerba *et al*. (1998) noted a much better time complexity for their path approximation than exact methods. Future work could systematically compare different approaches.

In conclusion, the q-grid VD is a useful method for modelling the spatial substructure within wildlife populations. It is especially useful in social species that form in groups with home ranges much smaller than patch size. Moreover, averaging population dynamics simulations over multiple q-grid VDs enables the construction of density maps that could be useful in wildlife management. This is particularly true because they pinpoint density to a specific spatial location.

7. ACKNOWLEDGEMENTS

We acknowledge the Australian Research Centre for Urban Ecology, The Baker Foundation, the Australian Research Council (LP0560443), VicRoads and the Albury Conservation Company.

8. REFERENCES

Chen, D.Z., R.J. Szczerba, J.J. Uhran, (1997), A Framed-quadtree approach for determining Euclidean shortest paths in a 2-D environment. *IEEE Transactions on Robotics and Automation*, 13(5), 668-681.

Dieckmann, U., R. Law, J.A.J. Metz, (2000), 'The Geometry of Ecological Interactions.' (Cambridge University Press: Cambridge, UK)

Hankski, I. (1999), 'Metapopulation Ecology.' (Oxford University Press: Oxford, UK)

Shaffer, C.A., H. Samet, (1987), Optimal quadtree construction algorithms. *Computer Vision, Graphics, and Image Processing*, 37, 402-419.

Szczerba, R.J., D.Z. Chen, J.J. Uhran, (1998), Planning shortest paths among 2D and 3D weighted regions using Framed-subspaces. *International Journal of Robotics Research*, 17(5), 531-546.

van der Ree, R., A.F. Bennett, (2003), Home range of the squirrel glider (*Petaurus norfolcensis*) in a network of remnant linear strips. *Journal of Zoology (London)*, 259, 327-336.