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Combining a dispersal model with network theory to assess habitat connectivity

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Abstract. Assessing the potential for threatened species to persist and spread within fragmented landscapes requires the identification of core areas that can sustain resident populations and dispersal corridors that can link these core areas with isolated patches of remnant habitat. We developed a set of GIS tools, simulation methods, and network analysis procedures to assess potential landscape connectivity for the Delmarva fox squirrel (DFS; *Sciurus niger cinereus*), an endangered species inhabiting forested areas on the Delmarva Peninsula, USA. Information on the DFS's life history and dispersal characteristics, together with data on the composition and configuration of land cover on the peninsula, were used as input data for an individual-based model to simulate dispersal patterns of millions of squirrels. Simulation results were then assessed using methods from graph theory, which quantifies habitat attributes associated with local and global connectivity. Several bottlenecks to dispersal were identified that were not apparent from simple distance-based metrics, highlighting specific locations for landscape conservation, restoration, and/or squirrel translocations. Our approach links simulation models, network analysis, and available field data in an efficient and general manner, making these methods useful and appropriate for assessing the movement dynamics of threatened species within landscapes being altered by human and natural disturbances.

Key words: *Delmarva fox squirrel; dispersal; graph theory; habitat connectivity; landscape corridors; Sciurus niger cinereus; threatened species conservation.*

INTRODUCTION

Habitat fragmentation is regarded as a primary cause of species endangerment (Czech et al. 2000, Kerr and DeGuise 2004), even though the separate effects of habitat loss and fragmentation on species persistence are difficult to ascertain (Fahrig 2003). The Delmarva Peninsula fox squirrel (DFS; *Sciurus niger cinereus*) was originally listed as endangered in 1967 because of a decrease in its distribution to about 10% of its original range. The dual pressures of over-hunting and habitat loss were the probable reasons for this population decline. Over the last 40 years, the abundance and distribution of this species has increased because of prohibitions against hunting, translocations of squirrels into new areas and natural expansion (U.S. Fish and Wildlife Service 2007). However, the question remains as to whether the forest that currently exists on the Delmarva Peninsula provides an adequately connected network that will enable the species to continue to spread into new areas. In addition, the peninsula continues to experience substantial land-use change. The long-term

resilience of the existing network of occupied patches to future change has not been studied in great detail.

The identification of critical landscape elements for promoting the reintroduction and spread of a species requires broad-scale assessments that link forest structural analysis (e.g., Riitters et al. 2002) and the functional responses of species to landscape pattern (e.g., Schumaker 1996). Quantifying this linkage using field tests requires extensive time and data to characterize species-specific responses to local details of landscape structure. Consequently, observational studies of individual dispersal outcomes are uncommon (Tyre et al. 1999, Kindlmann and Burel 2008; but see Larsen and Boutin 1994, Haughland and Larsen 2004). These difficulties are compounded when the area of interest is a broad geographic region and when large numbers of taxa are to be considered. In addition, experimental studies of the effects of fragmentation are not possible without actually disrupting connectivity, which is not in the interests of forest or wildlife management.

A computer-modeling approach provides a method for using limited existing data to assess the potential for connectivity problems for species at risk, and to locate critical regions where landscape change would most threaten connectivity. In particular, properly formulated simulation exercises can: inform management of the most relevant parameters and processes to measure in the field to improve future assessments; highlight

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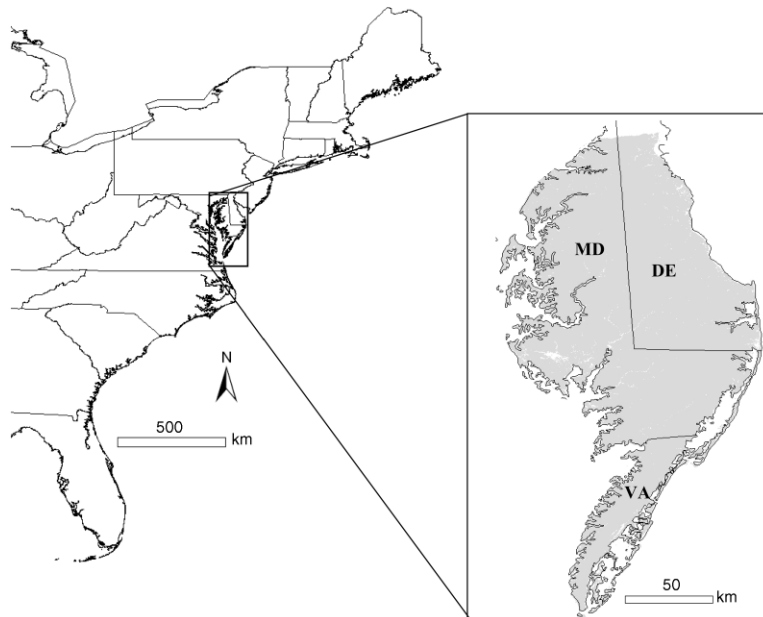


FIG. 1. Delmarva Peninsula (right panel blowup) encompassing parts of Delaware, Maryland, and Virginia in the eastern United States.

sensitive locations in the landscape from which field data are most needed; and identify specific landscape structures such as corridors that are most likely to either facilitate or impede inter-patch movement of a wide variety of organisms. Unfortunately, the statistical methods that can fit a random walk model to tracking data (e.g., radio or satellite telemetry; Jonsen et al. 2005) or estimate dispersal kernels from long-term mark-recapture data (e.g., Chapman et al. 2007) can not be used for the DFS due to the paucity of available movement data for this species.

Models of dispersal for the DFS, as well as many other endangered species, are often constrained by limited observations of actual dispersal events and limited information on how individuals perceive landscape features and adjust movement accordingly (Dunning et al. 1995). In these situations, individual-based, spatially explicit modeling approaches are a useful alternative for identifying landscape features that promote or restrict dispersal (Jopp and Reuter 2005, Kindlmann and Burel 2008). These methods have been extensively used for a variety of dispersal related issues, including the increased spread of invasive species and diseases as well as community and ecosystem restoration (DeAngelis et al. 1998, Berec 2002, Grimm et al. 2006, Nehrbass et al. 2007). However, the huge volume of data generated by these models can make analysis difficult. In this paper, we offer an efficient and objective set of methods for visualizing and interpreting model results using principles of graph theory (Harary 1969). By coupling the analytic tools of graph theory with landscape simulation modeling, we define critical areas (both habitat patches and corridors) that could be

important for the continued recovery and spread of this endangered species.

It is the purpose of this paper to demonstrate the utility of linking these methods and applying them to the DFS within the fragmented landscape of the Delmarva Peninsula. We first simulate the dispersal of squirrels using an individual-based dispersal algorithm especially adapted to multi-habitat, gridded, landscape data. These results are then analyzed within a graph theoretical framework to assess the potential connectivity in different regions of the landscape. The results are compared to those using inter-patch Euclidean distances as inputs for the connectivity assessment. The approach can be used to identify specific patches and corridors for conservation and targeted management to allow for more effective movement of squirrels across the fragmented landscape.

METHODS

Study site

The Delmarva Peninsula is a roughly 30 000-km² peninsula spanning parts of Delaware, Maryland, and Virginia in the eastern United States (Fig. 1). It is bordered by the Chesapeake Bay on the west and the Atlantic Ocean on the east. The Chesapeake and Delaware Canal cuts across the northern extent of the peninsula, making the area a virtual island from the perspective of a small, ground-dwelling mammal.

We used the 2001 National Land Cover Data (NLCD; Homer et al. 2004) downloaded from the Multi-Resolution Land Characteristics Consortium in grid format at 30-m resolution to characterize the landscape of the entire Delmarva Peninsula (Fig. 1).

TABLE 1. Land cover description for the Delmarva Peninsula, USA, the percentage of land area (water excluded) covered by each class, and movement (p_m) and mortality (p_d) parameter assignments for J-walk simulations.

Land cover description	Area (%)	p_m	p_d
Open water		0.00001	0.1
Developed, high intensity	0.23	0.001	0.01
Developed, medium intensity	0.61	0.001	0.01
Developed, low intensity	1.35	0.01	0.01
Emergent herbaceous wetland	10.56	0.01	0.01
Woody (non-forest) wetland	2.76	0.01	0.01
Developed, open space	1.83	0.1	0.01
Barren land†	2.10	0.1	0.01
Cultivated crops	34.23	0.5	0.0001
Pasture/hay	16.27	0.5	0.0001
Forested wetland	2.85	1	0.0001
Evergreen forest	5.33	1	0.00001
Mixed forest	1.54	1	0.00001
Deciduous forest	19.34	1	0.00001

† Barren land is rock, sand, and so on.

The NLCD data uses a modified Anderson Level II classification (Anderson et al. 1976) with 14 land cover classes found on the Delmarva (Table 1). The classification includes a woody wetlands designation where forest or shrubland vegetation is found on periodically saturated soils. We separated out the subset of these wetlands in forest cover using National Wetland Inventory (NWI) data and aggregated these “forested wetlands” with the deciduous forest, evergreen forest, and mixed-forest classes to create a habitat map for the DFS.

One of the most important practical and theoretical contributions of landscape ecology is the recognition of the importance of the patch to population processes within the fragmented landscape mosaic (Wiens et al. 1993, Andren 1994). We next analyzed the habitat map to identify forest patches using two alternative minimum patch size thresholds. Based on an earlier population viability assessment (Hilderbrand et al. 2007), a patch size of 400 ha was determined to be a conservative estimate of the forest area required to sustain an isolated population of DFS for 100 years. Populations of DFS are frequently found in smaller patches of forest on the peninsula, and we reduced the minimum patch size criterion to 175 ha in a final simulation scenario. This smaller patch size matches the lower bound provided in Hilderbrand et al. (2007), which assumes ideal habitat conditions and does not account for disturbance, climate change or any other stochastic variability. However, we chose to use patches of 400 ha as nodes for the majority of our scenarios, to insure that the resulting networks contain sufficient forest area for long-term persistence in spite of potential disturbance events (Hilderbrand et al. 2007).

Using the REGIONGROUP command in ArcINFO (ESRI, Redlands, California, USA), we applied the eight-neighbor (or next-nearest neighbor) rule to the habitat map to identify all contiguous habitat patches. We identified 148 forested habitat patches of 400 ha or

more on the Delmarva Peninsula. These 148 patches were designated as the subset of patches considered for the majority of dispersal simulations (Table 2, Fig. 2). The 148 suitable forest patches are scattered throughout the peninsula, in contrast to the current known distribution of DFS, which is concentrated in the western portion of the Delmarva. Unoccupied patches could be recolonized in the future, and thus confer a higher potential for the long-term persistence of the DFS. Changing the patch size to 175 ha resulted in 303 forest patches (Table 2).

The landscape graph

Graph theory (Harary 1969) is a branch of discrete mathematics used to analyze networks. Its rising popularity in the ecological literature includes applications to birds (Minor and Urban 2007), bats (Rhodes et al. 2006), amphibians (Lookingbill et al. 2008), insects (Jordan et al. 2003), plants (Neel 2008), corals (Treml et al. 2008), and small mammals (Bodin and Norberg 2007). The graph data structure (e.g., relative to raster-based data) is highly efficient for assessing networks of connectivity (see Hayes 2000a, b for a brief overview of graph theory applications to a variety of social and physical networks).

The landscape graph is defined by two basic elements: a map of habitat patches (or nodes) and a set of connections (or edges) among nodes. Thus, landscape graphs will be sensitive to the criteria used for defining the minimum patch size (PS) and determining network adjacency (AC, Table 2). We considered five different simulation scenarios that varied PS and AC. For most analyses (Scenarios 1–4), the landscape graph was defined using nodes representing a minimum forest patch size of 400 ha (number of forest patches, NP = 148). These scenarios differed only in their definition of

TABLE 2. Network metrics for five simulation scenarios.

Metric	Simulation scenarios				
	1	2	3	4	5
AC (%)	Euclidean (8 km)				
PS (ha)	400	400	400	400	175
NP (no.)	148	148	148	148	303
Simulation results					
NC	3	17	15	27	21
NE	577	213	236	181	525
IP	1	11	9	18	12
A_{LC} (km ²)	2.58	2.33	2.35	1.23	2.91
F^*	0.99	0.89	0.90	0.47	0.97

Notes: The scenarios differ in the criterion for determining network adjacency (AC) and the size (PS) and subsequent number (NP) of forest patches. Scenarios 2–5 were performed by releasing 100 000 dispersers from each patch. Key to variables: NC, the number of components, where a component is a group of connected patches; NE, the number of edges connecting network patches; IP, the number of isolated patches without edges connecting to other patches; A_{LC} , the area, in km², of the largest cluster; F^* , the ratio of A_{LC}/A_{TOT} , where A_{TOT} is the total amount of habitat in all patches.

network adjacency. For the final analysis (Scenario 5), PS was reduced to 175 ha (NP = 303).

The principal focus of this paper was the challenge of defining patch adjacency using a process-based dispersal model. The graph adjacency matrix \mathbf{A} is an $N \times N$ binary matrix where N is the number of nodes in the graph. The elements, a_{ij} , of the \mathbf{A} matrix are set to 1 if patch pairs are connected; to 0 if they are not connected. For Scenario 1, we set PS to 400 ha and defined AC as the greatest observed distance moved between sites for the DFS (8 km; Dueser 1999). If the distance between two patches, i and j , was < 8 km, then $a_{ij} = 1$ (connected); for distances > 8 km, $a_{ij} = 0$ (not connected). This simple rule using Euclidean distance for defining adjacencies is consistent with the most common method used to construct \mathbf{A} in the ecological literature (e.g., Urban and Keitt 2001, D'Eon et al. 2002, Rudd et al. 2002). However, the use of Euclidean distances may have little meaning for heterogeneous landscapes where movement success is affected by urban structures and aquatic barriers (Murphy and Lovett-Doust 2004). To account for the effect of matrix habitat structure (e.g., barriers preventing successful dispersal), the remaining four scenarios modeled the potential influence of land cover characteristics on DFS dispersal using an individual-based dispersal model.

J-walk simulations

J-walk is an individual-based simulation model of vertebrate dispersal within heterogeneous landscapes (Gardner and Gustafson 2004). Two maps are required by J-walk for each simulation: a land-cover map (in raster format); and a map of the locations of habitat patches from which individuals will be released and to which they may disperse (see landscape description in *Methods: The landscape graph*). J-walk then sequentially releases individuals from the edge of each home patch, records the pattern of movement through the raster landscape and summarizes the fate of all dispersing individuals. Interactions between dispersing individuals are not simulated in the model.

The individual-based movements are governed by a directionally biased, first-order correlated random walk (BCRW; see Gardner and Gustafson 2004). Correlated random walks produce the convoluted paths often demonstrated by dispersing organisms (Turchin 1998, Zollner and Lima 1999, Skalski and Gilliam 2003) with mean displacement controlled by the number of steps and the frequency of turns in direction. The J-walk algorithm, which operates in discrete rather than continuous space, produces BCRW with a four-step sequence repeated at each time step: (1) the direction of movement from the previous time step (or the "forward direction") is randomly deflected (see parameter C , described later in this subsection); (2) the land-cover dependent probabilities of movement (p_m) of the eight adjacent neighbors are assembled into a cumulative frequency distribution (cfd); (3) this cfd is multiplied by

the bias terms which maintain the forward movement (or momentum) of the dispersing individual and the cfd is then normalized to sum to 1.0; and (4) a random step to an adjacent site is then randomly selected from the normalized cfd. This sequence is repeated for each time step, moving the individual through the landscape until either a new patch is reached, a mortality event occurs, or the maximum number of steps (T) is exceeded.

The bias terms of the BCRW produce the forward momentum (i.e., the correlated walk) required to simulate species that move long distances across heterogeneous landscapes. Nevertheless, the BCRW still allows individuals to avoid or be attracted to local habitat features (simple, unbiased random movement does not result in a net displacement of individuals, see Turchin 1998, Skalski and Gilliam 2003). The bias terms in J-walk have been adjusted so that forward movement is twice as likely as a 90-degree turn and 20 times more likely than a 180-degree turn (see Gardner and Gustafson 2004 for additional details). We further adjusted the degree of deflection of the preferred direction of movement by calibrating the turning angle parameter (C) in the model using data obtained by direct observation of DFS movement events.

The J-walk movement algorithm assumes that dispersing individuals are able to detect habitat types within an approximately 1-ha area. The potential effects of detection distances on dispersal success have been widely considered for a variety of vertebrate and non-vertebrate species (see Pe'er and Kramer-Schadt [2008] for a review). Although attempts have been made to assess habitat detection distances for fox squirrels, *Sciurus niger*, detection distances beyond 300 m explained little of the variability in observed movement patterns ($R^2 = 0.18$; Mech and Zollner 2002). Because experimental data defining detection distances for the DFS (*Sciurus niger cinereus*) do not exist, J-walk detection distances were limited to the 1-ha assumption.

J-walk requires the estimation of two important movement parameters (T and C), and two sets of land-cover dependent probabilities (p_m and p_d , the probability of mortality). Likely ranges for these parameters can be inferred from dispersal observations and our general understanding of the life-history of the DFS. The first movement parameter, T , sets the maximum number of steps that an individual may make during a dispersal event. The assumptions used to derive this upper limit were that dispersal events are seasonal and of relatively short duration and that the rate of movement should be no more than 1–2 km/d. Combining this information, we allowed for a maximum total distance traveled of 15 km per dispersal event, or 500 steps on our 30-m resolution map. This distance was supported by radio-collar data tracking detailed movement for a handful of fox squirrels on the Delmarva Peninsula (Delaware Natural Resources and Environmental Control, *unpublished data*). Although dispersing

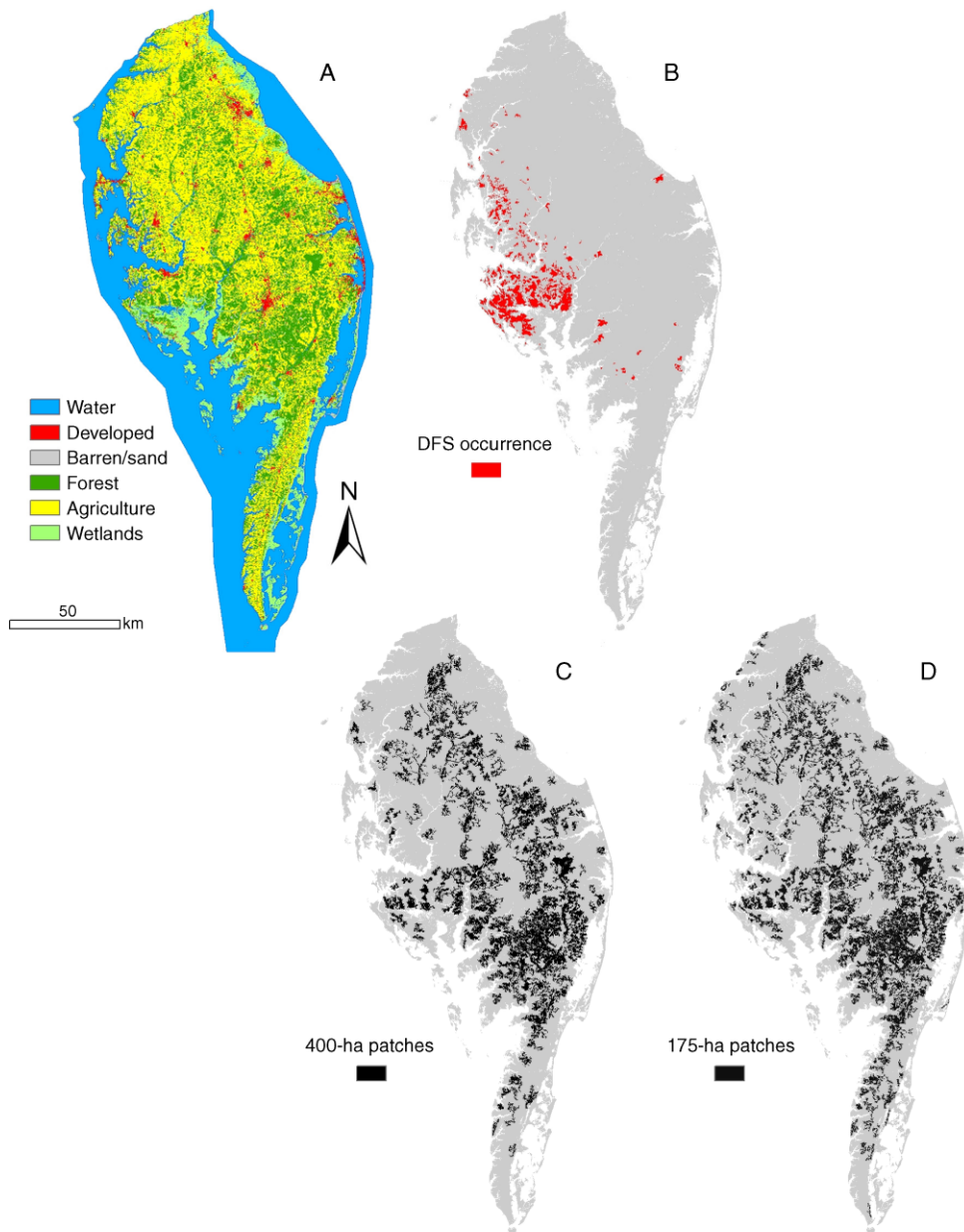


FIG. 2. Land cover, Delmarva fox squirrel (DFS) occurrence, and patch maps for the Delmarva Peninsula. (A) Land cover map with full set of land cover types condensed into six major classes; (B) locations of known DFS populations; (C) patches larger than 400 ha; (D) patches larger than 175 ha.

squirrels could move up to 15 km in total distance, this distance moved would not result in a net displacement of 15 km because of the complexity of the movement path.

The turning angle parameter in the model, C , randomly deflects the preferred direction of movement determined by the BCRW bias term, producing jagged paths typical of individuals exploring habitat to locate a new home range (Kareiva and Shigesada 1983, Turchin 1996, Jonsen et al. 2005). Dispersal distances are inversely related to C : high values of C within homogeneous landscapes produce a tortuous path with

low values of mean displacement; conversely low values of C will result in relatively straight paths and high values of mean displacement (see Fig. 3). We estimated values of C using information from a study of 231 tagged fox squirrels in Chincoteague, Maryland (Dueser 1999). Of the 22 that were observed to move between sites, the maximum observed net displacement distance was 8 km. Assuming 8 km to represent the 99th percentile displacement, we determined that when $C = 0.48$ only 1% of the walkers were displaced 8000 m from their starting point (Fig. 4).

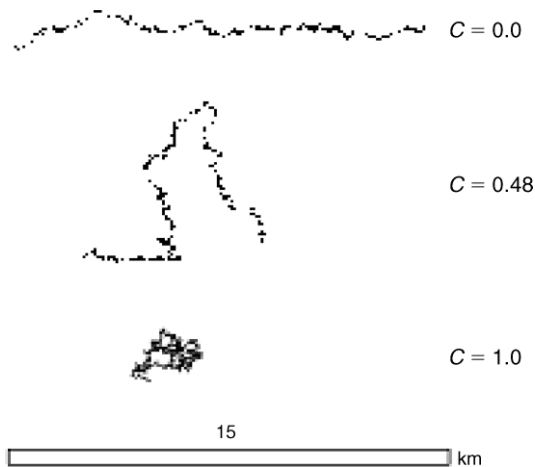


FIG. 3. Effect of turn angle parameter (C) on net displacement relative to total distance moved. A value of $C = 0.0$ yields “almost” straight-line movement with displacement approximately equal to the total distance moved (~15 km). A value of $C = 0.0$ provides net displacement of approximately zero. The value of $C = 0.48$ yields a net displacement of 8 km for 15 km total movement.

The probabilities of movement into adjacent sites, p_m (Table 1), at each time step were estimated by considering the preferred habitat types of the DFS. The Delmarva fox squirrel is most often found in loblolly pine (*Pinus taeda*), oak (*Quercus* spp.), or mixed deciduous forest (U.S. Fish and Wildlife Service 1993). Mature stands of large trees (>30 cm dbh) and open understory are preferred (Therres and Willey 2002). However, the DFS has also been observed in certain non-forested areas (e.g., pastures and cultivated fields) within their range (Adams 1976). Based on their collective experience working on the Delmarva, personnel from the U.S. Fish and Wildlife Service Chesapeake Bay Field Office and Maryland Department of Natural Resources assigned a rank order for the 14 land-cover types of our landscape maps from least preferred (open water) to most preferred (deciduous, coniferous, or mixed forest) and assigned corresponding values of p_m to each cover type (Table 1). The p_m values of the eight adjacent neighbors were used by the dispersal algorithm to guide each step taken by the walkers (e.g., given the choice a disperser would be twice as likely to move into an adjacent forest cell as a pasture cell). The relative probability of mortality, p_d , was also assigned for each cover type and used to determine mortality events following each step taken by a virtual disperser. These values were selected to provide a reasonable rank ordering of habitat preferences, because the precise values for multiple land cover types could not be derived from available data.

J-walk simulations were performed by releasing 100 000 individuals from randomly selected locations along the edge of each patch and recording the fate of the dispersing organisms. The actual number of

dispersers emigrating from any given patch is likely to be small and to vary as a function of patch size and quality (including stand age, species composition and stochastic factors). Our case is typical in that we did not have the data necessary to parameterize these variables for forest patches across the Delmarva Peninsula. Rather than estimating the prerequisite emigration rates for a metapopulation model, our goal was to estimate the probability of dispersal success independent of the actual number of dispersers from any given patch (e.g., to estimate the strength of potential connectivity as defined by Calabrese and Fagan [2004]). Consequently, to assure numerical accuracy, 100 000 dispersers were released from each patch.

The J-walk simulations provide information on successful transfers from source to destination patches that can be summarized in the adjacency matrix A of a landscape graph. For each pair of patches (i and j), the number of successful dispersers moving between the patches can be tallied. This tally can then be converted to the probability of successful dispersal based on the total number of dispersers released from the patches. If that fraction moving between the two patches was at least equal to the adjacency criterion, AC , then the patches were considered connected (i.e., $a_{ij} = 1$) and an edge was placed between them in the landscape graph. Basing the adjacency requirement on these dispersal probabilities rather than other GIS-based estimates of habitat heterogeneity such as least-cost path (e.g., Adriaensen et al. 2003) has the advantage of accounting for multiple alternative pathways through the landscape simultaneously. The approach also identifies landscape structural elements that act to funnel a large number of dispersers toward or away from successful pathways. This information can be extremely important in a management context. For example, a single pathway between patches that was hard to find or had many dead-end detours might not be a valuable corridor for conservation, even if it were relatively “low cost.”

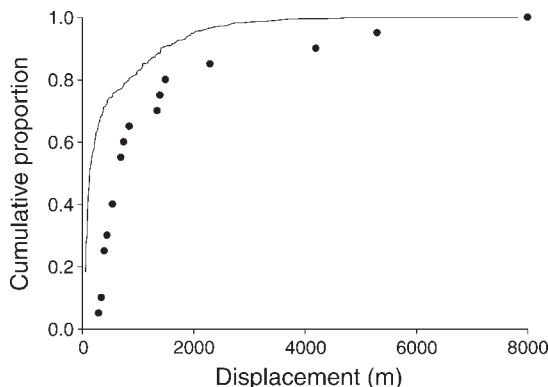


FIG. 4. Cumulative proportion of Delmarva fox squirrel movement vs. displacement distance. The solid line represents simulated movement. Symbols (dots) represent observations from Paglione (1996), Dueser (1999), and Bocetti and Pattee (2003).

The output from J-walk was used to build four landscape graphs (Table 2: Scenarios 2–5). Scenario 2 used the 400-ha forest patches (NP = 148) and recorded adjacency (AC) as at least 1% of the 100 000 dispersers successfully moving between pairs of patches. In practical terms, a 1% transfer implies that if, on average, 10 squirrels were to disperse from a given patch i every year, then at least one transfer would successfully reach patch j over a 10-year period.

Scenarios 3 and 4 examined the effect of AC, the dispersal threshold, on the resulting adjacency matrix, A. For Scenario 3, we reduced the threshold for creating an edge to 500 (0.5%) of 100 000 dispersers, while Scenario 4 increased this threshold to 2000 (2%). The minimum patch size and thus the number of patches (PS and NP, Table 2) was the same as in Scenarios 1 and 2. Because resident populations of DFS are known to occupy smaller patches than the 400 ha used in the first four scenarios, a final set of simulations was performed (Scenario 5) with the minimum patch size set to 175 ha (NP = 303) and the dispersal criterion, AC, set to 1%, the same as Scenario 2.

Graph analyses

By converting the raster output from J-walk to a graph we were able to take advantage of the powerful and well-defined connectivity algorithms from graph theory. These include both landscape-level analyses of connectivity and the identification of specific structural elements that promote or hamper connectivity.

For each graph, we calculated the following landscape-level network statistics: NC, the number of components; NE, the total number of edges, or adjacencies; IP, the number of isolated patches; A_{LC} , area (in km²) of the largest component; and F^* , the ratio of A_{LC} to A_{TOT} , the total amount of habitat in all patches (Ferrari et al. 2007). A component is defined as a group of connected patches (see Urban and Keitt 2001 for more details). The number of graph components, NC, is a measure of overall connectivity and ranges from 1 to NP, or the number of patches. In a landscape with only one component (NC = 1) all patches are accessible either directly or indirectly from all other patches. In a landscape with NC = NP, all patches are isolated. IP was calculated to complement NC by explicitly providing the number of components that consisted of single nodes. A_{LC} represents the aggregate area of the patches contained in the component with the largest area, or the area of the largest patch (whichever is greater). When NC = 1, $A_{LC} = A_{TOT}$ (i.e., all habitat in the landscape), and $F^* = 1$. Thus, F^* is a measure of connected habitat relative to the amount of habitat potentially available for inclusion in the network. Low values of F^* imply opportunities for increasing the connectivity of the landscape by forging connections with isolated habitat.

At the level of the individual edge, we conducted a series of edge removal exercises to identify specific

connections of greatest importance for connectivity. Previous landscape graph analyses have attempted to gauge the importance of losing specific patches to overall connectivity (e.g., Keitt et al. 1997). For the Delmarva Peninsula, we assume large unbroken forest tracts (>175 ha) may undergo disturbance but are unlikely to disappear entirely. Our concern was with the impact of increased development or other changes in cover classes in the matrix surrounding large patches and the impact of these changes on connectivity at the scale of the landscape graph. Therefore, instead of performing node, or patch removal exercises, we performed edge, or adjacency removal analyses.

To gauge the effect of losing adjacency between specific patches, we systematically changed the adjacency a_{ij} from 1 to 0 for each pair of connected patches and recalculated the graph metric A_{LC} for the resulting graph in the absence of this connection. Many edges in a network are redundant, and their loss has little relative impact on network connectivity. We were particularly interested in identifying those edges that either played a large role in connecting areas of known DFS occupancy to the rest of the landscape or were especially important to overall graph connectivity (i.e., “articulation edges” in graph theory). It is worth reemphasizing that because multiple dispersal pathways may exist between two patches, the adjacency criteria we specified treat the aggregate of pathways as a single connection, or edge. Therefore, the edge removal exercise accounts for real-world changes such as new shopping complexes or roads that would eliminate multiple pathways simultaneously.

Focusing on the nodes rather than the graph edges, we also quantified the relative importance of habitat patches using centrality metrics that have been promoted specifically for management activities like translocations (Jordan et al. 2007, Minor and Urban 2008). “Degree” is a measure of the number of adjacencies associated with a given node. This simple measure takes into consideration only first-order connections and is therefore a very local accounting of connectivity. For example, a satellite patch having only one connected neighbor has a degree of 1, while a central patch connected to 10 other patches has a degree of 10. “Betweenness” is a broader scale measure of overall landscape connectivity (Freeman 1977). It quantifies the number of shortest paths from each patch, i , to every other patch, j , that run through the focal patch, k :

$$\sum_i \sum_j \frac{g_{ikj}}{g_{ij}}$$

where g_{ij} is the number of paths from i to j and g_{ikj} is the number that run through patch k . Patches with high betweenness scores are theoretically used more often than patches with lower scores, and would therefore have a higher conservation value.

In addition to assessing centrality scores on a patch-by-patch basis, we examined the degree distribution (i.e., number of connections for each patch) generated

by the entire graphs relative to what would be expected of random networks (Bollobas 1985) and other well-studied graph structures (Watts and Strogatz 1998, Albert and Barabasi 2002). The shape of the degree distribution has been linked to the rate of spread of organisms through ecological networks (see Minor and Urban 2008). For example, degree distributions consistent with what would be expected of random graphs (i.e., Poisson distributions) indicate a graph with low clustering, which would support relatively constant rates of spread (Bollobas 1985, Jeger et al. 2007). A more skewed degree distribution, as might be expected from a scale-free network (Albert and Barabasi 2002), confers slow spread, unless or until a hub is encountered, at which time many patches can be reached simultaneously.

Network statistics for the five simulation scenarios (Table 2) were compared to evaluate the robustness of results. All analyses were done using a modified version of the Landgraphs software (Urban 2003), with the centrality measures as calculated in Pajek 1.23 (Batagelj and Mrvar 1998).

RESULTS

The landscape graph created by setting connections between nodes based on a Euclidean distance ≤ 8 km (Scenario 1, Fig. 5A) was dominated by three large components (NC) with 577 edges (NE, Table 2) and only a single isolated patch (IP, Table 2). The proportion of connected habitat was nearly 100% ($F^* = 0.99$, Table 2). By using simple Euclidean distance as the adjacency criterion, AC, this scenario ignores the effects of the heterogeneous structure of the landscape matrix as simulated by J-walk in the other four scenarios.

Each J-walk simulation scenario was performed by releasing 100 000 random walkers from each forest patch for a total of 14.8 million walkers for Scenarios 2–4 and 30.3 million for Scenario 5. The results for Scenario 2 (Fig. 5C) show that setting AC at 1% resulted in over two million successful node-to-node dispersal events producing 213 edges (NE, Table 2) between the 148 nodes. There was good agreement between empirical and simulated cumulative frequency distributions of distances moved with slight underestimates for the J-walk simulated displacements (Fig. 4). The difference between observed and simulated movement distances may be due, in part, to the fact that J-walk launches walkers and records dispersal success at patch edges. Observations of tagged squirrels were not restricted to edge-to-edge distances and may have included additional within-patch movements.

Examination of the cumulative distributions of dispersal distances (Fig. 4) shows that the majority of successful dispersal events involve movement distances that are far less than the 8-km maximum dispersal for the DFS. Even though these node-to-node distances are relatively short, the paths actually followed are consid-

erably longer. The behavior of dispersing squirrels and the structure of the landscape combine to produce convoluted dispersal paths. For example, when the straight-line distance between nodes equaled 1.0 km the mean distance that successful dispersers transversed equaled ~ 5.9 km.

Comparison of Scenario 1 (Euclidean distance scenario) with Scenario 2 also illustrates the effect of landscape structure on dispersal of the DFS. The network created as a product of the J-walk simulation had far fewer edges (NE = 213, Table 2) and a greater number of separate components (NC = 17). Six percent of the nodes for Scenario 2 were isolated (IP = 11), and the largest component for Scenario 2 was 25 000 ha less than for Scenario 1 (A_{LC} , Table 2). The specific locations where differences occur between Scenarios 1 and 2 are of interest. An examination of a small area of the peninsula where DFS are abundant (Fig. 5B, D) shows that the locations of towns and rivers had a significant impact on dispersal success.

The assessment of articulation edges using the network for Scenario 2 identified a handful of connections as particularly important for landscape-level connectivity (Fig. 6). Breaking any of these connections would substantially decrease the area of the largest component A_{LC} . It is especially noteworthy that these connections occur along the potential corridor linking areas of high DFS occupancy to large regions of unoccupied habitat. The opportunity for this pathway to act as a corridor facilitating spread of the species throughout the peninsula is emphasized by the high betweenness values of patches in this region of the map (Fig. 7).

Other important patches from Scenario 2 are those with high numbers of direct connections (i.e., high degree). The three patches with highest degree are the large patch in the southern portion of the peninsula and two smaller patches centrally located in a region of high patch density in the northern portion of the map (Fig. 7). The large, southern patch is located at the tail-end of cumulative frequency distributions of patch degree for all of our scenarios (Fig. 8A–D). In general, the form of the cfd was unchanged for the different scenarios and was consistent with what we would expect from random graphs. For example, the median degree for Scenario 2 matches that of a random graph created with the same mean and total number of edges (Fig. 8E), and is three times higher than would be expected for a scale-free graph (Fig. 8F). However, the three high-degree patches identified in Fig. 7 contribute to the skew of the distributions (e.g., skew of 2.2 for Scenario 2), which better matches that of scale-free (2.4) than random (0.3) graphs.

The number of edges, components, and isolated patches increased or decreased in predictable ways for Scenario 3 (AC = 0.5%) and Scenario 4 (AC = 2%), respectively (Table 2). The significantly smaller size of

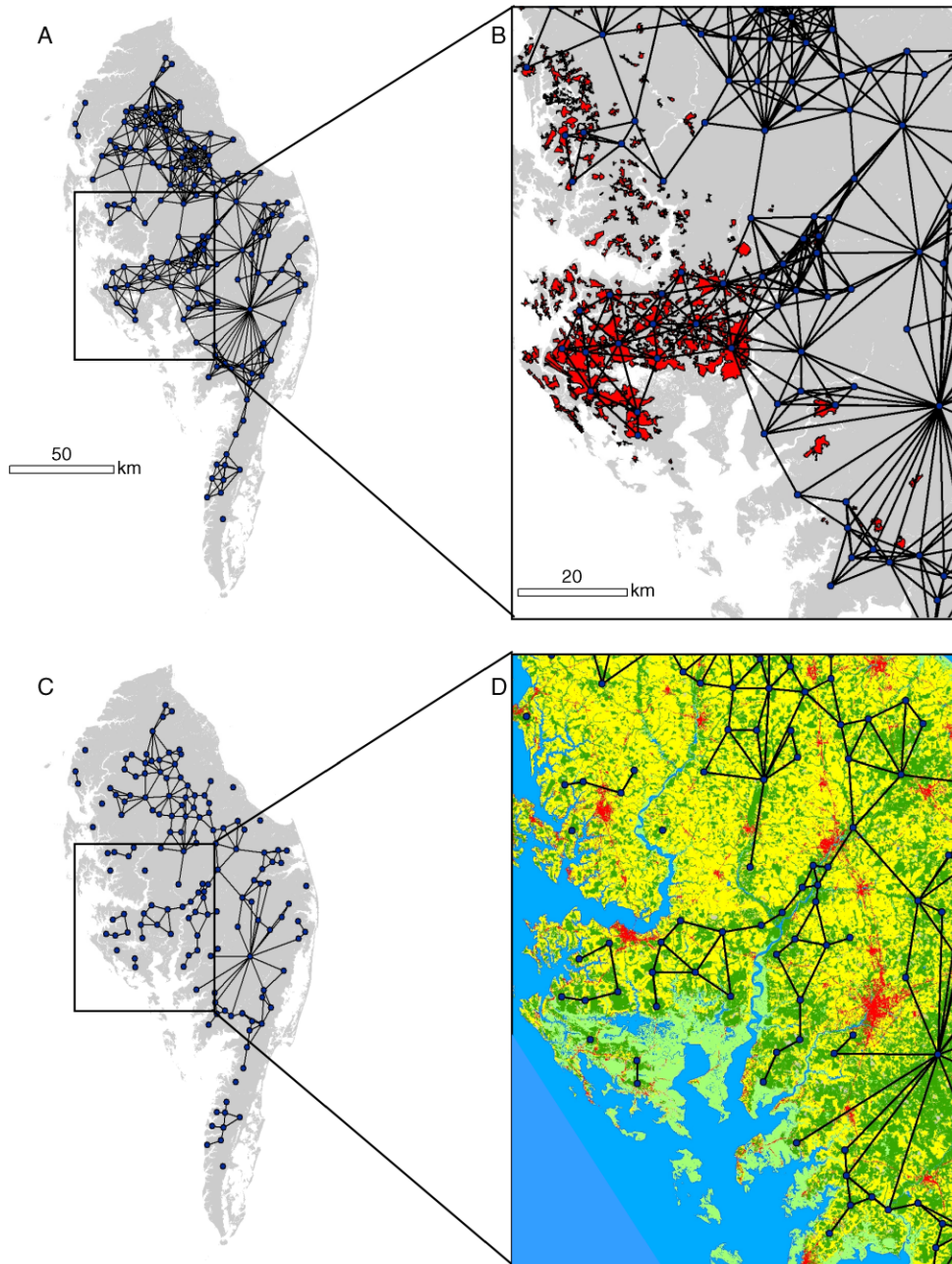


FIG. 5. Euclidean vs. simulation-derived networks (Scenario 1 vs. Scenario 2): (A) Euclidean network; (B) enlargement of region in panel A, showing Euclidean network with red indicating areas of occupancy for the Delmarva fox squirrel; (C) J-walk network; (D) enlargement of region in panel C, showing J-walk network with underlying land cover classification as per Fig. 2.

the largest cluster for the 2000 walker graph of Scenario 4 ($A_{LC} = 1.23 \text{ km}^2$; $F^* = 0.47$, Table 2) illustrates that the peninsula was effectively split into two separate networks with fewer than 2% of the simulated dispersers able to make the interpatch jump between the northern and southern components of the landscape.

Scenario 5 used the same adjacency rule as Scenario 2 ($AC = 1\%$ dispersal success) but included forested

patches with a smaller minimum area requirement ($PS = 175 \text{ ha}$). The number of edges and proportion of connected habitat were higher for Scenario 5 than any of the other J-walk scenarios, and more closely resembled those values from the Euclidean-based network (Table 2). Some of the additional, smaller patches included in this scenario acted as stepping stones creating new potential dispersal pathways. For example, increased movement around the town in Fig. 5D was possible and

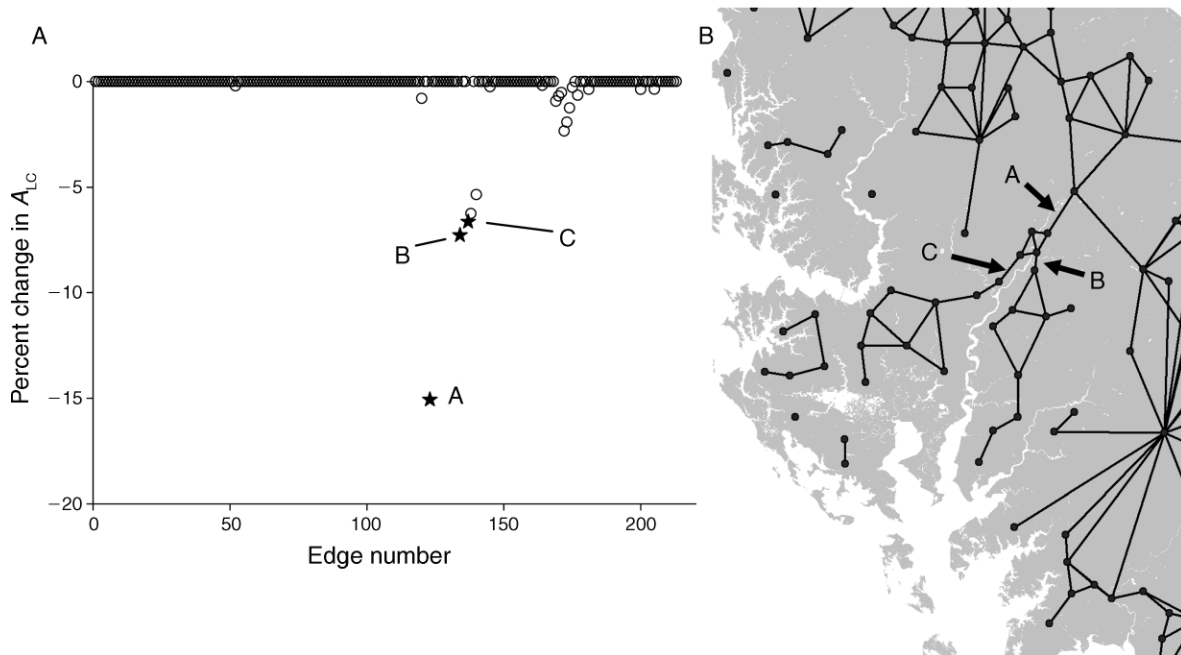


FIG. 6. Sensitivity of Scenario 2 to edge removal. (A) The change in the percentage of habitat contained in the largest component (A_{LC}) vs. the edge number removed (all symbols). Points A, B, and C (stars) represent the three greatest reductions. (B) The network with the corresponding links identified.

a new corridor connecting the area of high DFS occurrence to the rest of the landscape (Zone B, Fig. 9) could be drawn using this revised set of rules. In general, the connectivity is rather high between existing areas of DFS occurrence and the next closest patch that is unoccupied for this scenario.

DISCUSSION

The development of management strategies for species whose preferred habitat exists as fragmented parcels requires an understanding of the existence and effectiveness of potential corridors among habitat patches. Because the probability of local extinctions increases as the abundance of habitat declines, maintaining and improving connectivity has become an essential element of conservation planning (Crooks and Sanjayan 2006). The use of habitat corridors to facilitate movement through an otherwise hostile matrix is one commonly advocated option for mitigating the effects of landscape fragmentation (Simberloff et al. 1992, Beier and Noss 1998). For species like the DFS, landscape connectivity is especially important because effective pathways are needed to promote continued expansion of its range. The effective connection of scattered parcels of habitat is directly determined by the structural features of the landscape, including corridor position, width, length and distance between habitat patches (Downes et al. 1997, Perault and Lomolino 2000). However, the relationship between landscape elements that seem to connect habitat parcels and the actual use of these elements by organisms to disperse between patches is

difficult to assess because actual dispersal events are rarely observed.

Simulation provides an effective tool for leveraging sparse observations of species dispersal events. The simulation results reported here were robust across a range of simulation scenarios, however additional data would be desirable to fill in important gaps in information and reduce model uncertainties. For example, the potential barriers to dispersal relied upon the expert opinion used to assign habitat preferences and mortality probabilities for the different land cover types (Table 1) because there is no experimental data to define these parameters. Although J-walk is most sensitive to the rank ordering of habitat preferences, the degree of squirrel movement through non-habitat areas is not well known and can vary considerably by season (i.e., rivers may not be barriers when frozen). New data gathered as part of ongoing management activities could be used to refine the simulation parameters (e.g., habitat preferences, distances moved, and so on), which could lead to refined management recommendations consistent with the principles of adaptive management (Harris et al. 2003).

Additional uncertainties are associated with the criteria that we used to define habitat nodes in the landscape graphs (e.g., either 175- or 400-ha forest patches). Because the DFS is not a forest-interior obligate species the minimum size of a forested patch required for the establishment of a home range and successful reproduction is uncertain. Although small patches are more vulnerable to extinction events, small

patches play a critical role in dispersal and population expansion. Consequently, the 175-ha patch scenario may be more reflective of landscape use by the DFS, especially within regions dominated by riparian forest corridors. In the absence of more detailed data on DFS minimum area requirements, the more conservative 400 ha model provides important insights for management by identifying potential corridors and gaps in the landscape that would otherwise be obscured.

We provide one example of the type of information that could be extracted from simulation models to construct landscape graphs, but the simulations produced additional data that may also be useful depending on the research/management objective. For example, Treml et al. (2008) used a series of outputs from a spatially explicit biophysical model to generate graphs for the Tropical Pacific that quantify annual differences in connectivity of coral reefs. Circuit models also provide basic information on landscape resistance and potential travel paths that can be analyzed using graph theory metrics (McRae et al. 2008). Vogt et al. (2009) demonstrated how the data on individual movement pathways generated from J-walk could be used in a more focused analysis of connectivity for a smaller section of the Delmarva. For our assessment of the potential connectivity of patches at the scale of the entire peninsula, the specific details of the millions of individual movement pathways were summarized within the binary adjacency matrix prior to landscape connectivity analysis.

Landscape analysis to inform management options

The analysis reveals distinctly different levels of connectivity within different regions of the Delmarva Peninsula. Our results support the division of the Delmarva into at least six discrete connectivity zones (Fig. 9) with each zone characterized by the extent of DFS occupancy and connectance of habitat. While there are other relevant management factors not considered here, the results can be used to inform management plans that promote the landscape-scale dispersal of DFS among the largest forested patches of the Delmarva Peninsula.

Zones A and B (Fig. 9) represent linear regions of patchy forest extending from the region of high occupancy in the southwestern portion of the peninsula. These corridors are critical for promoting the spread of squirrels to unoccupied habitat throughout the peninsula (e.g., see decrease in the size of the largest graph component when connections within the zones were removed; Fig. 6). It is likely that squirrels are expanding from the historic population low in the mid-1960s (U.S. Fish and Wildlife Service 2007). However, because of the behavioral and life history limitations of the DFS, expansion of their range along these corridors has been slow. Therefore, the long-term maintenance of forest corridors in these regions will be important for continued population persistence and expansion.

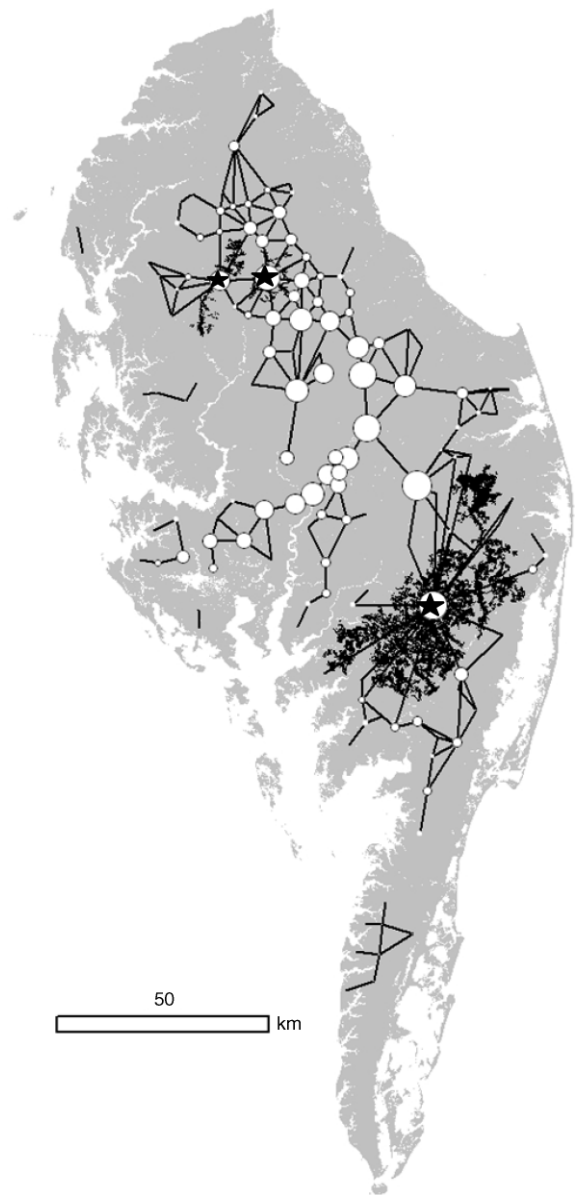


FIG. 7. Centrality measures for patches of the Delmarva Peninsula (Scenario 2). Black lines represent edges. Nodes are indicated as white circles located at centroid of the patch they represent. Diameters of the circles increase with increasing betweenness score. The three black stars represent the patches with highest degree; actual patches are shown in black underneath for these three critical nodes.

Zone C is dominated by human-created barriers to dispersal. Fewer than 2000 modeled dispersers successfully traversed this zone, which is fewer than required to draw an edge for the most stringent adjacency rule (Scenario 4 in Table 2). Only two edges were produced for this area using Scenario 2. The presence of these two edges substantially increases the size of the graph (e.g., F^* is nearly 50% greater for Scenario 2 than for Scenario 4; Table 2). A combination of matrix management

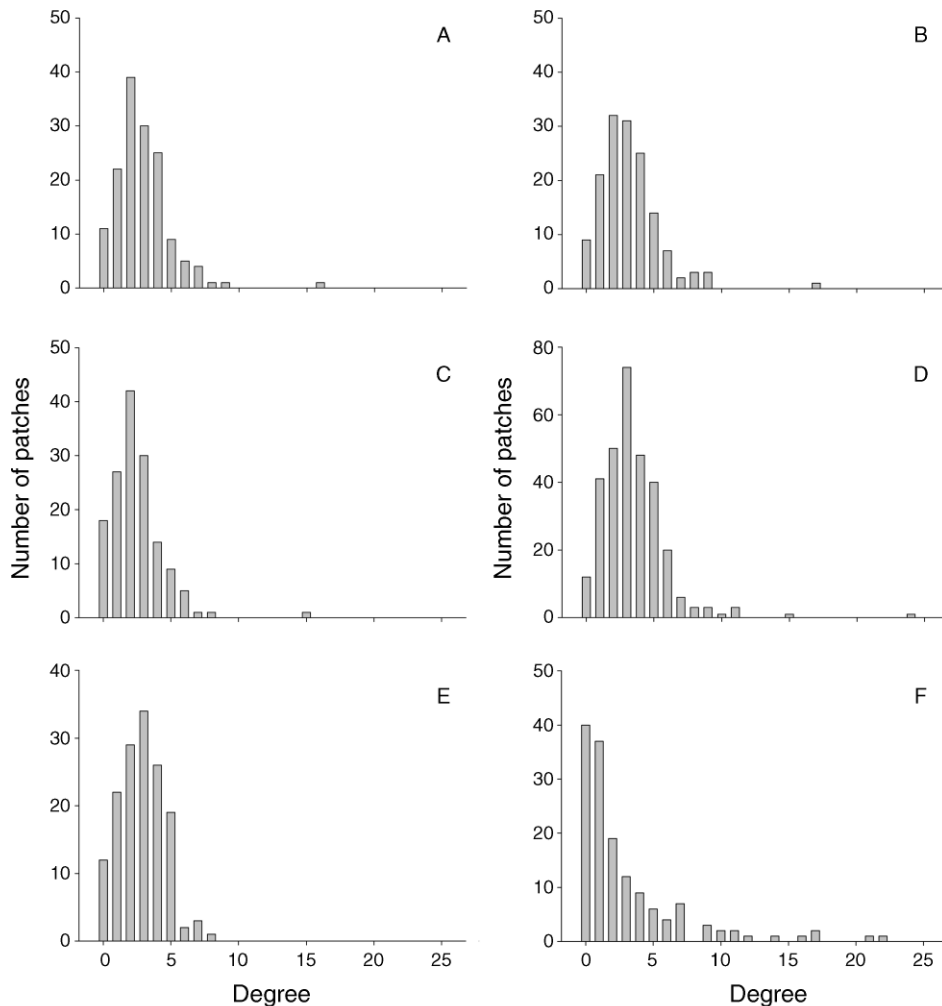


FIG. 8. Degree distributions for four different J-walk scenarios: (A) Scenario 2, minimum patch size, PS = 400 ha, adjacency threshold (AC) = 1%; (B) Scenario 3, PS = 400 ha, AC = 0.5%; (C) Scenario 4, PS = 400 ha, AC = 2%; and (D) Scenario 5, PS = 175 ha, AC = 1%. Panels E and F are for random and scale-free graphs, respectively, built using the same number of patches and edges as in Scenario 2.

strategies (e.g., forest buffer strips in agricultural fields) could be used to improve connectivity for this important region of the peninsula.

Zone D represents two forest patches in the north with no known DFS occupancy, and Zone E represents a patch in the south with only scattered DFS occupancy. Both of these regions have potentially high local connectivity (Fig. 7). Although attempts at translocating individuals have been unsuccessful for many species (Fischer and Lindenmayer 2000), DFS translocations have had a high level of success: 11 of 16 transplanted populations exist today (U.S. Fish and Wildlife Service 2007). The suitability of the large forest patches in Zones D and E to act as hubs for future translocations is indicated by the degree distributions of the landscape graphs (Fig. 8). These three high-degree patches slightly skewed the distributions as would be expected from scale-free networks, which have increased connectivity

at certain preferred patches (i.e., hubs). The resulting shape of the histograms corresponds with those built from landscape networks for bats (Rhodes et al. 2006) and birds (Minor and Urban 2008) in other regions of the world. Thus, we would anticipate a sharp increase in the rate of spread once these potential hub patches become densely occupied.

Finally, Zone F represents a large portion of the northwest quadrant of the Delmarva where DFS occupancy is high, but there are few contiguous forest patches larger than 400 ha. The simulations using the 175-ha patches (Scenario 5) indicate that Zone F has a strong network of these smaller forest patches including many that occur along streams and rivers. Field sightings of DFS indicate that they are frequently found in the riparian forests within this predominantly agricultural region. Management activities that conserve or enhance riparian forests in this zone would be

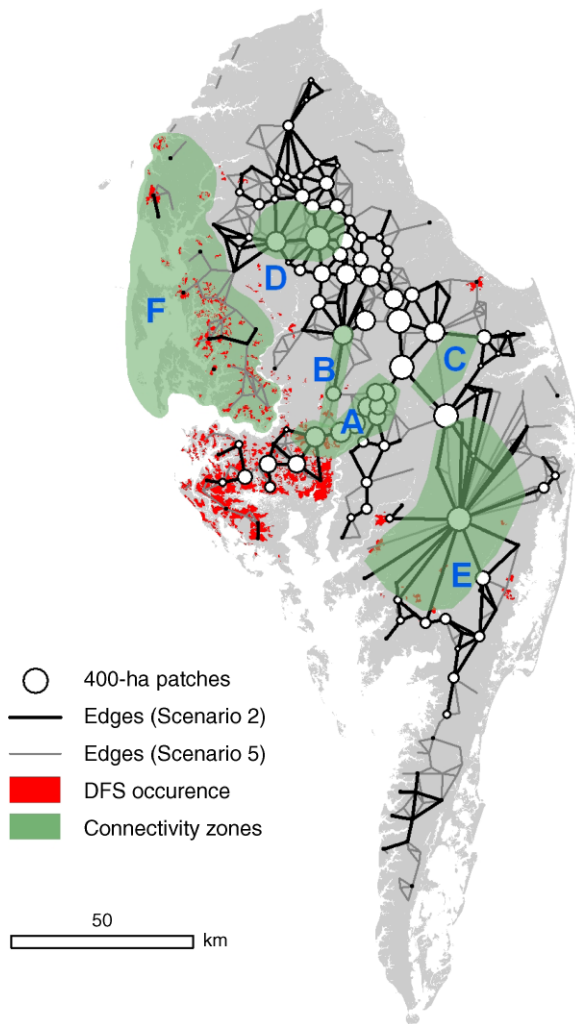


FIG. 9. Proposed connectivity zones for the Delmarva Peninsula. Zones A and B indicate potential corridors for DFS spread from area of high current occupancy. Zone C represents an area of high regional connectivity value threatened by anthropogenic barriers to dispersal. Zones D and E represent areas of high local connectivity that are currently unoccupied. Zone F is an area of high current DFS occupancy with few patches greater than 400 ha. (Circles representing patches are scaled by their network betweenness scores.)

beneficial to the DFS as well as other wildlife species of regional concern, such as forest interior birds (Robbins et al. 1989, Keller et al. 1993).

Conclusions

The fragmented forest of the Delmarva Peninsula provides an excellent case study for examining how model simulations can be used to parameterize a network analysis. The DFS is a forest-dwelling, endangered species with an expanding range (U.S. Fish and Wildlife Service 2007). Due, in part, to its endangered status, data on the dispersal of the DFS is perhaps as good as or better than could be expected for most

vertebrate species. Nevertheless, available data have not been sufficient to characterize the dispersal patterns of this species over the range of conditions found in the Delmarva Peninsula. Simulation tools such as J-walk provide a helpful way of leveraging sparse data to evaluate potential patterns of movement under a variety of conditions. However, the enormous quantity of information that can be generated by these simulations (e.g., millions of dispersal events over hundreds of habitat patches) can be difficult to interpret.

We have used the adjacency matrices of graph theory as a parsimonious method of data distillation and analysis. Graph theory based network analyses are becoming increasingly popular in ecological studies (Calabrese and Fagan 2004). In most cases, the adjacency matrix, A , is defined by comparing the Euclidean distance among patches to the gap-crossing ability of a given species (sensu Urban and Keitt 2001). When empirical data from field studies are insufficient to draw a complete picture of landscape connectivity, individual-based simulation methods, as we have used here, provide an alternative method for estimating species-specific connectance pathways through heterogeneous landscapes.

The approach presented here can be easily extended to other species, either native species recovering from disturbances or exotic species invading new habitat. The approach of coupling a dispersal model with network theory can also be easily extended to assess the potential effects of proposed management or development scenarios on the connectance of fragmented populations. For example, our edge removal exercise systematically removed each edge, one at a time, from the landscape graphs. If specific combinations of edges were threatened (e.g., by a large-scale land conversion project), these scenarios could be quickly evaluated. Taken as an analytic package, these methods provide a valuable instrument for understanding the relationship between landscape patterns and species persistence and spread.

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