

Research Article

A practical map-analysis tool for detecting potential dispersal corridors*

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Received 27 August 2003; accepted in revised form 10 September 2004

Key words: Connectivity, Fragmentation, Matrix, Metapopulation, Movement, Network, Patch, Preserve design, Sink, Source, Travel path

Abstract

We describe the Pathway Analysis Through Habitat (PATH) tool, which can predict the location of potential corridors of animal movement between patches of habitat within any map. The algorithm works by launching virtual entities that we call ‘walkers’ from each patch of habitat in the map, simulating their travel as they journey through land cover types in the intervening matrix, and finally arrive at a different habitat ‘island.’ Each walker is imbued with a set of user-specified habitat preferences that make its walking behavior resemble a particular animal species. Because the tool operates in parallel on a supercomputer, large numbers of walkers can be efficiently simulated. The importance of each habitat patch as a source or a sink for a species is calculated, consistent with existing concepts in the metapopulation literature. The manipulation of a series of contrived artificial landscapes demonstrates that the location of potential dispersal corridors and relative source and sink importance among patches can be purposefully altered in expected ways. Finally, potential dispersal corridors are predicted among remnant woodlots within three actual landscape maps.

Introduction

Habitat connectivity plays an important role in the viability of species populations by increasing effective population size, maintaining gene flow, and facilitating regular migration, dispersal, and recolonization (e.g., the ‘rescue effect,’ Brown and Kodric-Brown 1977). Each of these processes helps ensure the long-term persistence of a population.

Insofar as they facilitate connectivity, movement corridors also foster persistence of species on the

landscape. The importance of corridors for wildlife movement in the conservation and management of biodiversity is acknowledged widely, from a theoretical perspective (Forman 1983, 1995; Dramstad et al. 1996) and through simulation approaches (e.g., Anderson and Danielson 1997).

Simberloff and Cox (1987) point out, however, that few empirical studies are available either to support or to refute the value of corridors in conservation management. Simberloff et al. (1992) suggested that corridors could actually harm species by facilitating the spread of diseases and parasites, or by concentrating prey species, thereby making them more susceptible to predators.

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Simberloff et al. (1992) argue that scarce conservation resources should be spent to increase the size of habitat patches rather than to create movement corridors of habitat between them. They stress the importance of small, nearby patches of habitat in a 'stepping stone' configuration, and argue for case-by-case management at a landscape scale. No tools exist which are suitable for the practical management of the habitat configuration of real landscapes.

All else being equal, a connected landscape is preferable to a fragmented one (Beier and Noss 1998, Bennett 1999). Natural landscapes are generally more connected than landscapes altered by humans, and corridors are a viable strategy to retain or enhance this natural connectivity (Noss 1987). Nevertheless, corridors must be evaluated individually on their own merits; theoretical considerations cannot be applied universally. No abstract discussion of corridors can adequately guide all management decisions (Simberloff and Cox 1992). Whether corridors are an appropriate management strategy can be answered only by considering ecological factors specific to a species and a site. Efforts must be devoted to solving actual management problems in real-world landscapes (Noss 1987).

A number of empirical studies now exist of corridors that have been purposefully created. Such studies usually distinguish between habitat patches that are suitable for the focal species and the rest of the environment, often called the matrix. One definition allows a corridor to be a commonly traversed route within a single habitat patch. Existing anthropogenic corridors like fencerows (Riffell and Gutzwiller 1996) or contrived clearcuts created within a forested matrix (Haddad and Baum 1999; Haddad 2000; Tewksbury et al. 2002) have been studied as corridors comprised of linearly shaped habitat patches.

Such linear habitat corridors have species-specific effects. Using three experimental landscapes clearcut into a loblolly forest matrix, Haddad and Baum (1999) observed that the presence of clearcut corridors dramatically increased dispersal ability for two species of open-habitat butterflies. Working at the same experimental site, Danielson and Hubbard (2000) found that the presence of cut corridors only weakly decreased the probability that old-field mice, *Peromyscus polionotus*, would disperse from a patch. The 32 m wide corridors

created for the study may have themselves represented patches of usable habitat for the mice.

Dunning et al. (1995) reported that corridor configurations improved the ability of Bachman's sparrow (*Aimophila aestivalis*) to find and settle in newly created patches, suggesting that, for species that do not disperse easily through inhospitable landscapes, habitat occupancy at a regional scale can be enhanced by careful landscape design and planning. Sisk and Haddad (2002) translated the theoretical benefits of corridors into recommendations for management practices.

Forman (1995) and Dramstad et al. (1996) suggested that long, thin corridors of habitat may serve as a 'drift-fence,' filtering individuals from the inhospitable matrix habitat and funneling dispersers into some patches. Isolated patches may be shielded by such a corridor-patch complex, and thus receive fewer dispersers. Haddad and Baum (1999) found that a drift-fence effect occurred in the clearcut patches, differentially concentrating some species of open-habitat butterflies. Danielson and Hubbard (2000), however, detected no drift-fence concentration effect for *P. polionotus* within the same experimental clearcut patches.

Here we ignore movement within single habitat patches, and define corridors as pathways through the matrix connecting at least two different patches of habitat. Defined in this way, a corridor is a frequently traveled pathway taken by an individual outside its' most preferred habitat. This alternative definition of corridors highlights habitat suitability not as a binary attribute, but as a continuum of usability. This definition of corridors is consistent with the theory of island biogeography (MacArthur and Wilson 1967), graph theory (Cantwell and Forman 1993), and the metapopulation concept (Levins 1969).

A metapopulation is a number of discrete local breeding populations occurring in distinct habitat patches that are connected by migration (Hanski and Gilpin 1997). Local population dynamics occur on a fast time scale in comparison with interpatch dynamics. Pulliam (1988) distinguished 'source' patches from 'sink' patches, based on whether emigration from a habitat patch exceeds immigration, or vice versa, at reproductive and dispersal equilibrium. A source patch has a positive local recruitment rate (birth minus death) in the absence of immigration, and thus provides a net surplus of emigrants. By Pulliam's (1988)

definition, a sink population may decline to a low but positive reproductive equilibrium in the absence of immigration. Other researchers define sinks as populations that would go extinct in the absence of immigration. A large proportion of a metapopulation can exist in sink habitats, if the source patches are sufficiently productive to subsidize the sinks. Pulliam and Danielson (1991), Pulliam et al. (1992), and Pulliam (1996) offered empirical evidence for the existence of such landscape-level, source/sink population dynamics.

Currently, no analytical tools exist which can predict comprehensively where potential dispersal corridors are likely to exist in real-world landscape maps, or which habitat patches will be sources and sinks. Island biogeography and graph theoretic approaches consider only the distance between habitat patches, without considering the spatially heterogeneous impedance of the matrix to movement. Diffusion equations (Okubo 1980) and percolation analysis (Stauffer and Aharony 1992) simulate a dispersal wave of organisms or an epidemic moving through a heterogeneous matrix, but cannot incorporate habitat-dependent differential animal feeding and mortality.

One alternative approach for finding potential corridors is to use the 'least-cost path' tools built into modern GIS systems (Walker and Craighead 1997, 1998). These tools, which were designed to find the cheapest geographic pathways for constructing a road between two points, use a theoretical cumulative cost surface constructed outward in all directions from the destination. Walker and Craighead (1997, 1998) used least-cost pathways to simulate movement corridors by calculating a cumulative cost surface based on habitat preferences for several target species, including grizzly bears, mountain lion and elk in Montana. Their approach assumes that animals will follow an optimum route between two points that minimizes their exposure to intervening low quality habitat. Movement would be facilitated by such routes, whether animals actively follow them or not (Walker and Craighead 1997).

The Southeastern Ecological Framework Project, sponsored by the Environmental Protection Agency, used GIS-based least-cost path tools to identify connectivity between ecologically significant areas within eight southeastern states. 'Linkages' between ecologically significant 'hubs'

were determined by creating a single cost surface for each of three type and size classes for hubs, and then using a GIS to find the least-cost path between each pair of hubs. GIS technicians buffered outward from each individual least-cost path, since they tended to converge to a single path to the destination, even when the source locations were varied (John Richardson, EPA, personal communication 06/2004). They buffered outwards from the solitary least-cost path into appropriate land cover, varying the width of the buffer by one of the three cost surfaces (Carr et al. 2002). Finally, all linkages are added together into a single map.

In a seminal paper, Gustafson and Gardner (1996) developed a Monte Carlo individual-based dispersal model using self-avoiding random walkers to measure immigration and emigration rates between habitat patches within a heterogeneous landscape matrix. Large numbers of dispersing individuals of a modeled organism were simulated as walkers traversing a land cover map from one habitat patch to another. Probabilities of movement into each land cover type were varied to reflect habitat preferences of the target species. Visualizations showed the visitation frequency of successful dispersers for each grid cell in the map.

Using random walkers, Gustafson and Gardner (1996) were able to quantify the exchange of dispersing individuals across the landscape. Their random walker model could determine potential instantaneous connectivity as in percolation analysis (Stauffer and Aharony 1992), while using movement preferences as in an individual-based model. Gustafson and Gardner (1996) found that transfer rates between two patches in each direction often were not symmetrical, because of the funneling effect of certain landscape patterns.

While able to measure the patch-to-patch flow of dispersers, Gustafson and Gardner's visualization of corridors on the landscape was unable to identify discrete travel paths used by successful dispersers when moving between habitat patches. Their Figure 7 shows potential occupancy around habitat patches, but does not explicitly locate successful dispersal pathways among them, even for patches that are nearly adjacent. Gustafson and Gardner (1996) concluded that 'corridors are diffuse and difficult to identify on the landscape.' Processing time for the computationally intensive

Monte Carlo walker model also proved to be problematic. Their serial code, run on a contemporary workstation, took 4 h to process a realistic 200-by-200 cell landscape in which the habitat patches had been simplified. Use of the random walker method for large, complex, realistic landscapes in a management context was not possible. Thus, Gustafson and Gardner's initial tool was experimental rather than practical. A subsequent paper emphasizes the walker method for testing the relative effect of landscape pattern and species characteristics on reintroduction success rather than delineation of movement corridors (Gardner and Gustafson 2003).

Here we report the development of a practical Pathway Analysis Through Habitat (PATH) tool for the detection of potential corridors in complex realistic landscapes. Based on random walkers, the PATH tool runs in parallel in order to provide the computational efficiency needed to analyze large landscapes with many habitat patches. Three products are produced by the PATH tool: (1) a map of the most heavily traveled potential movement pathways between patches of each analyzed map category, (2) a square transfer matrix quantifying the flow of animals successfully dispersing from each patch to every other patch, and (3) a set of importance values for every patch in the map which quantifies the contribution of that habitat patch to successful animal movement across the map. The transfer matrix is square and not triangular, since the rate of animal movement is likely to be asymmetrical between any two habitat patches. An importance value is calculated for each patch, independent of reproduction, which is consistent with Pulliam's (1988) source/sink population concept. Exchange of individuals among patches is used to calculate a reproduction-independent source and sink importance for each patch. Patch importance is given in the form of both a matrix of flow and a color-coded patch map.

Methods

The corridor detection method

Our algorithm works by launching virtual walkers from each patch of habitat in the map, simulating their travel as they journey through land

cover types in the intervening matrix, and finally arrive at a different habitat 'island'. Each set of walkers is imbued with a set of user-specified habitat preferences which make their movement behavior resemble that of a particular animal species. Because the PATH tool operates in parallel, large numbers of walkers can be efficiently simulated.

Habitat patches are the landscape unit of concern, and all patches are treated equally, regardless of their area. Only walkers which successfully disperse (i.e., which actually reach another patch of habitat) are retained. After walkers have been launched from all habitat patches, the collected footprints of all successfully dispersing walkers are inversely weighted by the energy used, and summed so that their combined tracks show the most heavily used pathways of movement across the map.

A map of the land cover or habitat categories must be supplied as input to the PATH tool. A second map in which individual, spatially contiguous patches of each category are encoded must also be supplied. The user supplies four types of additional habitat-specific information: preferences for each type of habitat, energy costs of movement through each type of habitat, likelihood of finding food in each habitat, and likelihood of mortality (other than starvation) in each type of habitat. The PATH tool allows separate preference specifications for multiple species of walkers, or for each sex or life stage of the animal being simulated.

Each walker is started at a random cell within its patch of origin, and is given a fixed amount of energy proportional to the size of the map. A 'hotfoot' routine makes the patch of origin distasteful, encouraging walkers to leave the patch of origin quickly and never return. Walkers which return to their patch of origin die, and are not included in the tabulation of dispersers or the mapping of dispersal corridors. These modifications increase the computational efficiency, since meandering inside or looping back to the patch of origin does not help delineate potential corridors.

The direction of the next step is determined by a habitat preference-biased set of probabilities, but the decision is made using a random number jump into those probabilities. Thus, walkers will occasionally step into low-preference, low-quality habitat, even if highly-preferred habitat is

available within one step. This movement mechanism allows for a potential dispersal corridor to form even through low-preference habitat, assuming that the rest of the travel path is short, and maximizes time spent in highly preferred habitat types. An ‘anti-vibrate’ routine discourages walkers from abrupt reversals by decreasing probability of movement back to their last position, or the two subcardinal locations on either side of the last. This gives walkers some directional momentum, and prevents movement oscillations that would spend compute cycles without serving to delineate potential corridors.

Three exclusive options are provided for the behavior of walkers at map edges: walkers encountering an edge can (1) die and have their tracks eliminated, (2) bounce off the edge as a wall, or (3) cross through the edge to re-enter the map on the opposite side. This last option wraps the map like a torus in two directions. Thus, the map appears infinite to walkers, eliminating the effect of edges on the corridors. While not likely to be useful in practice, the option can be used to test for the presence of an edge effect.

Only tracks of walkers that successfully reach another patch of habitat are used to map potential corridors. Walkers may fail to disperse because they re-enter their patch of origin, encounter the map edge under the edge-die option, or because they exhaust their movement energy. Additional walkers are started from a patch until a user-determined number of walkers have successfully dispersed. Each node of a cluster computer is assigned a patch of origin from which to send walkers in parallel. A fixed success quota keeps the sampling intensity constant, giving all patches an equal chance to contribute to the formation of potential dispersal corridors.

A computer node may be assigned a patch which is surrounded by a barrier, or is particularly disconnected from the other patches. To prevent the node from endlessly sending walkers, it aborts that patch after sending a certain number of walkers without attaining the success quota. The ‘abort quota’ is like the detection limit for an analytical device, except that it is under the user’s control. A patch which has reached the abort quota has less than the specified Minimum Success Ratio (MSR), and therefore has a level of connectance which is less than the detection limit.

Calculating source and sink importance of habitat patches

We calculate, for each habitat patch, a relative measure of the ease with which walkers may disperse from a given patch to somewhere else, and the ease with which a walker may disperse to the same given patch from somewhere else. These relative measures of source and sink importance, respectively, are consistent with the terminology of Pulliam (1988), except that they are independent of within-patch reproduction. Thought of another way, these source and sink importance values are what would be expected if population recruitment within each patch was equal. No reproduction is simulated in the instantaneous potential connectivity modeled by the PATH tool.

Source and sink importance for a patch are calculated in independent ways. Source importance is calculated as the ratio of successful dispersers originating in the patch to the total number of walkers (whether successful or not) sent from the patch. Successful walkers originating from aborted patches are counted toward source importance even though the MSR is not met for that patch. Sink importance for a patch is calculated as the ratio of successful dispersers ending up in the patch (having started from some other patch) to the number of all successful dispersers originating from all habitat patches. Successful dispersers from aborted patches make no contribution to sink importance.

Concepts of source and sink importance, as used here, can be succinctly stated in four axiomatic rules:

1. Successful walkers from each patch (including aborted patches) contribute to the source importance of their patch of origin.
2. Successful walkers from each patch do not contribute to the source importance of any other patches.
3. Successful walkers from each patch do not contribute to the sink importance of their patch of origin (i.e., walkers die if they return to their patch of origin).
4. Successful walkers from each patch contribute to the sink importance of other patches only if the MSR for their patch of origin is met (i.e., successful walkers from aborted patches are not counted).

As a result, traversals from aborted patches count only toward the source importance of their patch of origin; they make no contribution to the sink importance of other patches (see rule 4). No footprints of walkers from aborted patches are used in the corridor map.

Summing footprints of successful walkers to form maps of corridors

Before they are summed, footprints of successfully dispersed walkers are weighted inversely by the square of the energy expended during their traversals. Thus, the most efficient traversal paths contribute more strongly to defining the most probable corridors. Footprints of walkers from each patch are accumulated, and the subset of corridors leading from each patch can be examined individually if desired. Corridor intensity from each patch is normalized before summing the corridors from all patches together, so that all patches contribute equally to the final map of landscape corridors.

Results

Experiments with simple artificial landscapes

We tested the behavior of the PATH tool on simple artificial landscapes designed so that the geographic arrangement of potential dispersal corridors could be intuitively predicted. No patches were aborted in any of the artificial landscapes. These test landscapes have a largely homogeneous matrix, with only a few intervening land cover types contrived to direct dispersal corridors in some expected way. Corridors through complex landscapes are not likely to be as intuitive, but PATH potential corridor results will be accepted more readily if the tool has shown appropriate behavior with simple, designed landscapes. Resource managers will need to experience such confidence-building experiments before fully vesting in the tool, so these efforts are important for acceptance and use.

Consider a landscape containing five, equal-sized patches of suitable habitat arranged like the side of a die within a homogeneous matrix (Figure 1*i*). Walkers die if they touch the edge of the map. In

this spatial configuration, diagonal pathways involving the center patch are the shortest, and are therefore detected as the strongest corridors, although vertical and horizontal pathways are also present, appearing as lateral blue wings on Figures 1*i D, E, and G*. As expected, the center patch is both the most important source and the most important sink.

Now consider the same landscape as Figure 1*i*, but with the edge-wrap option set, so that walkers leaving any map edge reappear on the opposite side of the map (Figure 1*ii*). The strongest corridors are now between the corner patches, especially in the top-to-bottom direction. Corner patches are slightly closer to the edges vertically than horizontally (Figure 1*ii B and C*), making the top-to-bottom corridors the strongest.

Figure 1*iii* shows the effect of removing the center habitat patch with the edge-die option set. Strongest corridors are detected horizontally (the shortest path), and strong corridors are also detected vertically. The yellowish hole in the middle indicates that somewhat weaker diagonal corridors are also present, and these diagonal pathways are visible in Figure 1*iii D through G*.

Figure 2*i* establishes a reference landscape to evaluate the effects of introducing a second land cover type within the intervening matrix between habitat patches with the edge-die option set. With a homogeneous matrix, the three main corridors form a triangle, with slight disperser concentrations just inside each of the habitat patches. The two top patches are slightly stronger sources, while the single bottom patch is a slightly stronger sink, because of the triangular arrangement of the patches in the landscape.

When a diagonal dispersal barrier is introduced into the matrix of the landscape in Figure 2*ii*, dispersers concentrate asymmetrically in corridors along the bottom side and off the free end of the barrier (Figure 2*ii*). The barrier funnels dispersers preferentially between the top right patch and the bottom patch (Figure 2*ii E and F*). As a result, the upper right patch becomes the strongest source, while the bottom patch becomes the strongest sink. This landscape illustrates the drift-fence phenomenon of Forman (1995) and Dramstad et al. (1996).

Figure 2*iii* shows how corridors are affected by four barriers forming a paired funnel configuration. Intense corridors are formed along the upper surfaces of each funnel, and in the throat. The

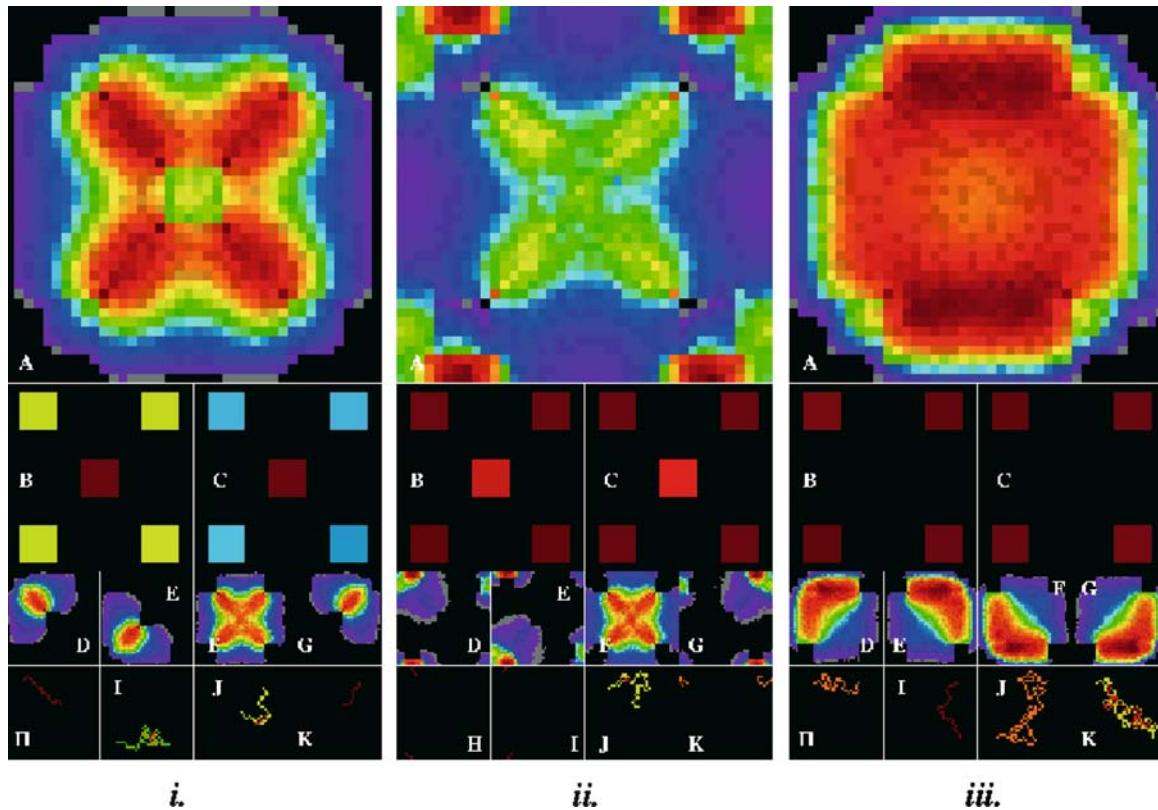


Figure 1. Corridor results within three contrived artificial landscapes (i–iii) containing habitat patches arranged within a homogeneous matrix. Dark red corridors are densest, through cooler colors to black (A). Maps of patch source importance (B) and patch sink importance (C) are also shown for each landscape. D through G show corridors leading from four of the individual habitat patches, and H through K show example tracks of successfully dispersing walkers, weighted by the inverse of squared track length Figure 1*i*. Five patches arranged as on a die. The edge-die option is set. Diagonals involving the center patch represent the strongest corridors between habitat patches (1*i*A), but vertical and horizontal corridors are also present. The center patch is the most important source (1*i*B), and also the most important sink (1*i*C). Figure 1*ii*. The same patch configuration as Figure 1*i*, but the edge-wrap option is set, so that walkers moving off one edge re-enter the map on the opposite side. Top-to-bottom wrapping pathways between corner patches now represent the strongest connections between habitat patches (1*ii*A), but the left-to-right connection is also present, as are the diagonals involving the center patch. The four corner patches now have the highest source importance (1*ii*B) and sink importance (1*ii*C). Figure 1*iii*. The center habitat patch is removed. The edge-die option is set. This landscape shows strongest horizontal corridors, but also shows strong vertical corridors and weaker diagonal corridors (1*iii*A). All four patches are roughly equal in source importance (1*iii*B) and sink importance (1*iii*C).

barriers improve top-to-bottom connectivity by directing dispersers toward appropriate patches, while leaving horizontal connectivity unchanged. Consequently, the paired top patches are the strongest sources, while the bottom patch is the strongest sink.

Detecting corridors in realistic landscapes

We obtained the same three realistic landscapes from the Kankakee River area in northwestern

Indiana that Gustafson and Gardner (1996) used in their random walker study. These landscapes show remnant fragments of deciduous forest within a predominantly agricultural matrix. Derived from Landsat TM images, they contain 11 land cover types, and were simplified by them to reduce the total number of habitat patches. We used the habitat preferences of a hypothetical species that Gustafson and Gardner (1996) specified in their maximum heterogeneity case. Habitat preference of this species increases from water to road, dry bare soil, bare soil, moist bare soil,

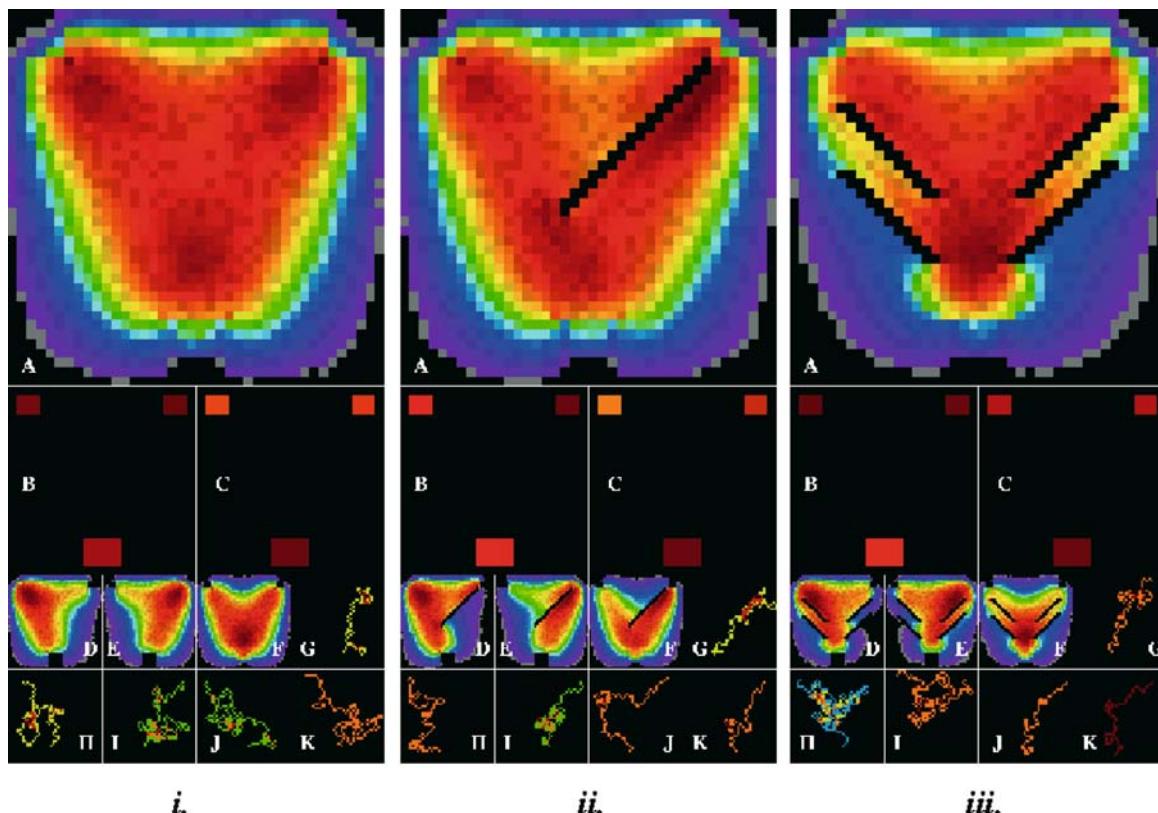


Figure 2. Corridor results within three contrived artificial landscapes containing three habitat patches arranged within a homogeneous matrix. A through K are defined in Figure 1. The edge-die option is set. Figure 2*i*. Corridors detected in this landscape form a heart or triangle, and are densest just inside each habitat patch (2*i*A). The two top patches are slightly stronger sources (2*i*B), but the single bottom patch is a slightly stronger sink (2*i*C). Figure 2*ii*. The matrix contains a diagonal barrier to disperser movement. Corridors detected in this landscape are still roughly triangular, but now dispersers are concentrated in a corridor along the bottom and off the end of the barrier (2*ii*A). The upper right patch is the strongest source (2*ii*B), while the bottom patch is the strongest sink. Corridors formed from individual patches, shown in 2*ii*D through 2*ii*F, show how this asymmetry occurs. Figure 2*iii*. The matrix contains paired diagonal barriers forming a nested funnel configuration. Corridors are concentrated by the barrier configuration, and are densest just above the lower patch, in the double throat of the funnel (2*iii*A). The upper two patches are the strongest sources (2*iii*B), while the lower patch is the strongest sink (2*iii*C).

young row crop, short grass, medium grass, tall grass, conifers, and deciduous forest (see Table 3, Gustafson and Gardner (1996) for probabilities).

PATH was used to determine corridors among deciduous woodlots within the 'MINE' landscape (Figure 3*i*). Strong potential dispersal corridors are predicted skirting around the edges of the ponds, connecting the three sets of habitat patches. Dispersers are particularly concentrated along the southern edge of the lower pond, as they pass between the lower habitat patches. This is not the only corridor between these patches; a more diffuse, dendritic pattern can be seen favoring the tall grass in the matrix. The patches to the east of the

ponds are connected by distinct pathways on both sides of the road curving downward from the gravel pit. The corridor to the east of the road is tenuous, following the tall grass. The corridor along the west side of the road is broader and stronger. The large patch in the southwest corner is poorly connected to the group of three patches in the northwest.

Strong, short corridors exist between the three northwestern patches, and between the two patches in the southeastern group, despite the presence of the road. The largest southwestern patch is the poorest source, but the northeastern patch is the poorest sink. If the gravel pit operation

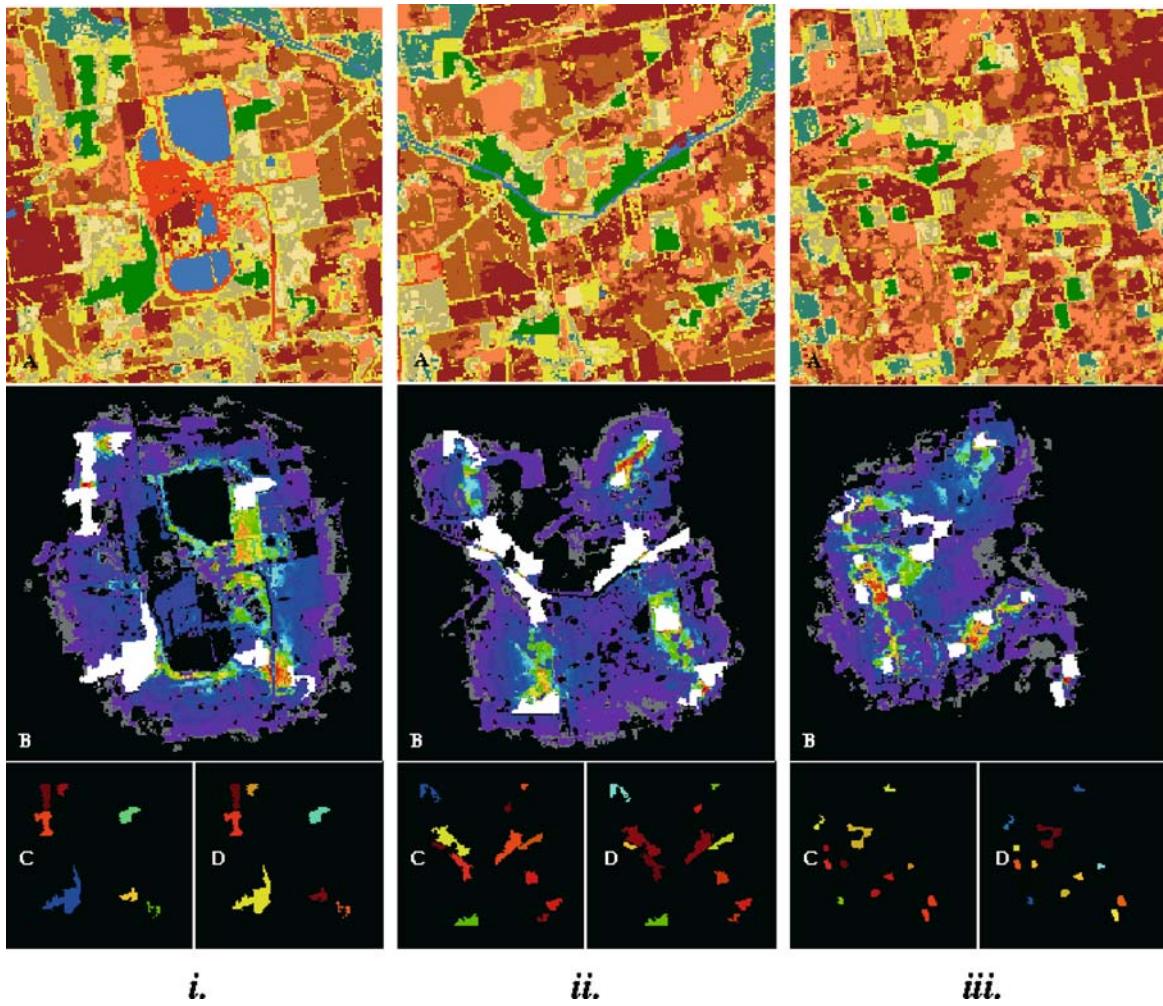


Figure 3. Three actual landscapes from northwestern Indiana analyzed for corridors. Green areas are remnants of deciduous forest (the habitat under analysis) within an agricultural matrix (A). Medium blue areas are water, browns are bare soil classes, and cream colors are grass categories. Light blue areas are conifers. Corridors detected among the remnant deciduous forest patches (B) are colored as in previous figures. Habitat patches are shown in white, and patch source importance (C) and sink importance (D) are also shown. Landscapes originally published in Gustafson and Gardner (1996), used with permission from E. Gustafson. Figure 3*i*. The 'MINE' landscape. The red area in the center of the image is a gravel pit operation. Figure 3*ii*. The 'RIVER' landscape. Figure 3*iii*. The 'AGRI' landscape.

destroyed any deciduous forest habitat patches, or if it created the ponds, it is likely that it substantially reduced the connectivity between the northwestern patches and the southeastern habitat patches for species migrating through this landscape.

Several large patches are divided by water in the 'RIVER' landscape, shown in Figure 3*ii*. Even though water is the least preferred cover type, strong corridors still exist through the river. Because of the proximity of these patches, the few walkers that manage to swim across and

successfully reach the habitat patch on the other side create a strong potential corridor. Inter-patch distance does not fully explain corridor development, however. The two patches in the northeast corner are about as far apart as the two largest patches in the southeast corner, yet the former are well-connected by short grass along the shoulders of a roadside. The habitat patch in the northwest corner is poorly connected to the other patches, since a wide area of drier bare soil isolates it, making it the weakest source and sink.

Grass growing along roadsides and section lines enhances connectivity across forested patches in the ‘AGRI’ landscape (Figure 3*iii*). Corridors to the top habitat patch in ‘AGRI’ are very interrupted and diffuse, making this patch one of the weakest sources and sinks in the map. The large grassy area between this top patch and the largest patch serves to dilute dispersers, even though the grass land cover is preferred.

Discussion

We assume that preferred high-quality habitat makes a better corridor than less-preferred habitat. We also assume that short connectors are used more than longer dispersal routes. The resolution of the habitat map may affect the delineation of potential corridors. Animals may functionally select resources at a finer scale, and this may not be the same path as one which is optimized by PATH at a coarser resolution. On the other hand, animals may respond to coarser-grained landscape cues than are represented by our habitat map, especially when migrating or dispersing across long distances. Movement choices and behaviors, even for a particular species, may vary with age, gender, pregnancy and nutrition status, and the nature and composition of traveling groups. If known, preferences for animals under specific circumstances can be used with the PATH tool to generate specialized potential movement corridors.

Unlike Gustafson and Gardner (1996), our visualizations clearly show potential travel paths used for dispersal. Although sometimes diffuse, these potential movement corridors are sometimes well localized and distinct, especially between nearby habitat patches. The inverse cost weighting and patch normalization are probably responsible for our successful resolution of geographic pathways.

Experiments using artificial landscapes indicate that resource managers can change relative source/sink strengths at will by altering the matrix through which dispersers must pass (Figure 2). These changes in source and sink strength can be made without changing the number, area, or spatial arrangement of the habitat patches themselves. Source and sink strengths are comparable across different maps,

since they are expressed as ratios, but greater numbers of walkers produce more precise estimates. Less than 1 min was required to simulate 10,000 successful walkers to detect corridors in the realistic landscapes using four nodes of a modest parallel computer. The weighted visualizations show distinct corridors through the realistic landscapes (Figure 3).

For realistic heterogeneous landscapes, it is usually difficult to guess before using the PATH tool where corridors will be located on the map, or which patches will be the most important sources or sinks. In a homogeneous matrix, potential corridors follow the shortest paths of least resistance, as might be expected. Indeed, potential corridors in the artificial landscapes resemble arcs of electrical current, or magnetic lines of force. Figure 3 shows purple halos surrounding all of the white habitat patches, indicating groups of patches that are connected by potential dispersal routes. High preference land cover types along roadsides and fencerows appear as preferred movement routes even when located far from habitat patches. The heterogeneous matrix of a realistic landscape contains habitat types with widely different impediments, making the corridors difficult to imagine before they are predicted.

In practical use, resource managers may need to creatively pre-process the habitat map before submitting it for corridor analysis. If the target organism has minimum patch area requirements, the map should be re-coded, changing patches that are smaller than this minimum to a separate cover type which can be assigned a lower preference. Maps submitted for species requiring core areas should have the peripheral parts of all patches re-coded and assigned lower preference values. Shallow parts of rivers and narrow parts of roads can be re-coded and assigned higher movement likelihoods.

A simple diffusion equation might have sufficed to find corridors through each of the six landscapes in Figures 1 and 2, in which the matrix is fairly simple (and such an equation might have been more efficient computationally!). However, it is unlikely that a diffusion equation could have been used to find corridors through the complex matrix in the realistic landscapes. Using random walkers, we can add realistic, habitat-dependent variable energy costs, energy gains, and mortality.

Least-cost path methods consider only one kind of cost surface, whereas PATH can simultaneously consider differential preference, movement cost, food availability, and mortality. More importantly, because they only show a single final pathway, least-cost path methods show only the current optimal route, but do not show secondary routes that could be made better than the current best route by making a small modification to the habitat map. The PATH tool shows all potential connectivity routes, not just the single current best. These promising, but currently secondary, pathways are just the ones of which resource managers need to be made aware. They need to be able to see landscape configuration situations where strategic management alterations will result in dramatic improvements in connectivity among habitat patches. Such places will be evident in the PATH output corridor map as strong potential corridors that are weakened in only one or two geographic locations by passing through low-quality habitat.

For example, the spatial combination of gravel pit roads between two large ponds in Figure 3*i* restricts corridors from passing through this area, and substantially reduces the northwest-southeast connectivity between the remaining forest fragments. Seeing that potential corridors skirt the two ponds, a resource manager could enhance the remaining connectivity by planting tall grass along the pond edges. A subsequent PATH analysis on the improved habitat map would show increased numbers of successful dispersers in the transfer matrix moving between the northwest and southeast groups of forest patches. The increase in successful potential dispersers would quantify the improvement made by the management action on the landscape. In this way, the PATH tool can be used as a ‘what-if’ tool to evaluate prospective changes in the landscape before they are made. PATH should also be useful in the design and maintenance of preserves consisting of several habitat remnants.

Individual random walkers are not analogous to individuals of the target species. Individual animals are much more sophisticated than walkers. All successful walkers taken together, however, represent a spatial optimization process which can be used to reproduce the optimum pathways that we expect the individuals of the target species to use most often, precisely because they are so well adapted.

For the same reason, it is not problematic that animals that may vary widely in the extent of their sensory range are represented by walkers having an ability to see only the habitat types immediately adjacent to their current location. The single step look-ahead assumption does not affect the optimization of the potential corridors found by PATH. The optimization in our method comes through the collective action of the large number of (only) successful dispersers, and the weighting of the most efficient potential dispersal paths the most heavily.

Even if we gave individual walkers a greater look-ahead ability, the same optimum potential corridors would be predicted by the PATH tool. Consider a situation in which the local environment is inhospitable; however, just beyond this, there exists a high-quality habitat pathway to another patch. Although short-sighted, a few walkers will make rare suboptimal choices and will cut through the inhospitable bottleneck to discover the optimized pathway beyond. Becoming successful dispersers, their tracks will be heavily weighted in the final map, showing the connection just as surely as if they had been able to look beyond the local problem.

The same behavior works in reverse. Pockets of higher quality habitat that are surrounded by barriers of poor quality habitat will attract many individual walkers. These walkers, however, will not be likely to successfully reach another patch. Since only the travel paths of successful dispersers are used, no potential corridors will pass through this attractive dead-end area, just as if walkers had been able to see the movement barriers that lie beyond. The weighting of potential corridors by energy expended, along with the normalization by habitat patches, ensures that the appropriate relative strengths of all potential corridors are preserved.

Corridors found using random walkers need to be validated and verified against actual movement corridors that have been experimentally observed. Radio tracking and telemetry studies should provide an opportunity for an empirical test of walker-generated corridors against observations of real species moving across actual landscapes.

Few resource managers have access to a supercomputer (but see Hargrove et al. 2001). We are developing a web interface for the PATH tool, so that users will have access to corridor analysis

without the necessity of owning a parallel supercomputer. Users will be prompted via the web interface to submit their map, full preference parameters, and the categories in the map which are to be analyzed for corridors. When their analysis is completed, users will be able to pick up their corridor results on a special web page. The web front end will make corridor analysis easily available to resource managers, representing an accessible form of technology transfer.

Acknowledgments

This research was sponsored by the National Petroleum Technology Office, U. S. Department of Energy, and by the Southern Appalachian Information Node of the United States Geological Survey National Biological Information Infrastructure program, and was performed at Oak Ridge National Laboratory (ORNL). ORNL is managed by UT-Battelle, LLC, for the U. S. Department of Energy under contract DEAC0500OR22725. We thank Nancy Comstock, Kathy Stirling, and Daniel Gurney, NPTO project managers, and Mike Frame, NBII project manager, for their support of this project.

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