Critical Linkages Phase II:

A Strategic Assessment of Increasing Regional Connectivity in Massachusetts Via the Installation of Wildlife Passage Structures

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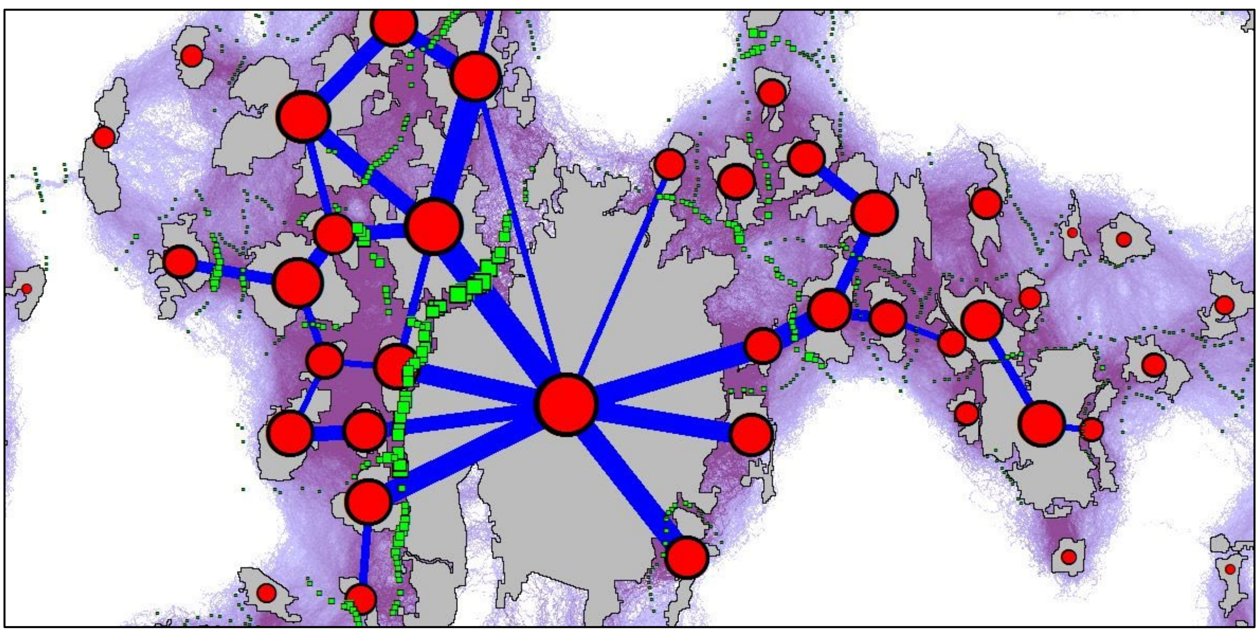

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Introduction

Connectivity across the landscape is important for all wildlife species. Connectivity matters at multiple scales: at a local scale, animals need to be able to move around within their home ranges and disperse to new habitat. At a broader, regional scale, dispersal over many generations allows species to shift or expand their ranges. Changes in distribution will become increasingly important as climate change makes large areas of former habitat no longer suitable for many species. For such long distance dispersal to be possible, the landscape must be interconnected for terrestrial species. Roads, agriculture, and suburban development all fragment the landscape, reducing connectivity at all scales. At the broad, regional scales that matter most for range expansion, roads are generally the most significant barriers, due to mortality from vehicles, behavioral avoidance, and, for smaller animals, physiological barriers (Forman et al., 2003).

The Critical Linkages Project

In the Critical Linkages project, we have been working in partnership with The Nature Conservancy to produce a comprehensive analysis of areas in Massachusetts where connections must be protected and restored to support the Commonwealth's wildlife and biodiversity resources. The Critical Linkages project consists of spatially explicit tools, including models, maps and scenario-testing software, with the goal of helping to assess how to mitigate the impacts of roads, railroads, and dams on the environment.

Critical Linkages builds on the Conservation Assessment and Prioritization System (CAPS, McGarigal et al. 2011). CAPS produces an ecosystem-based “coarse-filter” assessment of ecological integrity for all ecological communities across the landscape. The results can be used to prioritize areas for biodiversity conservation. The coarse-filter approach does not involve any particular focal species but instead holistically considers ecological systems.

Because we are dealing with biodiversity in its broadest sense we distinguished two important scales for assessing connectivity, which we refer to as local and regional scales. Local connectivity refers to the spatial scale at which the dominant organisms interact directly with the landscape via demographic processes such as dispersal and home range movements. Regional connectivity refers to the spatial scale exceeding that in which organisms directly interact with the landscape. This is the scale at which long-term ecological processes such as range expansion/contraction and gene flow occur.

Phase I of the Critical Linkages project focused on analyses of local scale connectivity while phase II focuses on assessing connectivity at the regional scale.

Critical Linkages I

In Phase I of the Critical Linkages project (McGarigal et al., 2012) we used the scenario testing capabilities of CAPS to assess changes in the local connectedness and aquatic connectedness metrics for dam removal, culvert/bridge replacement projects and construction of wildlife passage structures on roads and highways. We assessed potential improvements in aquatic connectivity by sequentially upgrading each road-stream crossing to a bridge, and removing each dam, and calculating the resultant change in local aquatic connectedness. Likewise, we assessed potential improvements in local terrestrial connectivity by sequentially inserting a wildlife passage structure on selected road segments, and calculating the resultant change in connectedness. These increases in connectedness/aquatic connectedness give an estimate of the improvement in local connectivity available for each potential infrastructure upgrade, taking into account both local effects (change in traffic and stream passability) and the landscape context. Results of the Critical Linkages I analysis are described in McGarigal et al. (2012) and available at https://umasscaps.org/applications/critical-linkages.html.

Critical Linkages II

In this second phase of the Critical Linkages project, we move to the assessment of potential increases in regional connectivity due to the construction of one or more wildlife passage structures on roads and highways. There are three major distinctions between Phase I and Phase II of Critical Linkages: (1) Phase II focuses on regional rather than local connectivity, (2) Phase II can assess the combined effects of multiple infrastructure changes, and (3) due to methodological constraints of the current algorithm, Phase II focuses only on terrestrial connectivity.

Because effective wildlife passages structures are expensive to install and maintain, a focus on regional connectivity makes the most sense. It is unlikely that hundreds of such structures will be built across Massachusetts in coming decades, so we argue for a strategic focus on a few locations that matter the most for regional connectivity, with its broad-scale and long-term ecological effects. Additionally, in some locations, restoring regional connectivity may require the concurrent construction of multiple wildlife passage structures. This second phase addresses both of these issues.

The entirely grid-based representation used in Phase I is computationally infeasible for larger regional scales (in general, the computational requirements of our connectivity metrics scale to the fourth power of the distance considered). In Phase II, we move to a hybrid graph-theoretic representation (Urban and Keitt, 2001), which yields high computational efficiency at these broad scales. We repeat the analysis at several scales (2, 5, and 10 km), representing dispersal abilities of different groups of species. Results of the analyses allow the assessment and visualization of regional connectivity throughout the landscape (both in local detail and in a landscape-wide schematic), the importance and irreplaceability of links in the landscape, and finally, an assessment of the potential increase in regional landscape connectivity to be gained by building wildlife passage structures on each segment of roads and highways.

Methods

The Critical Linkages II analysis consists of a number of steps, summarized here, and described in detail below. The analysis focuses on connecting *conservation nodes* ("nodes" for short), which are areas selected to represent existing or anticipated high-quality habitat. Sections of roads where wildlife passage structures could be built to improve connectivity among nodes are designated as *contingent units*. A large number of *random low-cost paths* are constructed through a *resistant landscape* between each pair of nodes, representing paths that might be taken by terrestrial and semi-terrestrial wildlife. The cost distance of each path is measured using a resistant surface, and the distance is converted via a Gaussian function into a *link probability* for a series of given bandwidths representing varying dispersal abilities. The sum of link probabilities across space gives the *conductance index*, representing the probability that a dispersing animal might pass through a given point in the landscape.

The landscape is then translated into a *graph*, based on a *graph-theoretic framework* (Urban and Keitt, 2001), in which nodes are connected by links (in the graph theory literature, links are called "edges," but we consider this term too confusing, and use "links" instead). Our conservation nodes are used as the nodes, with a value based on their size and ecological integrity. The mean link probability is used as the links among nodes. We use Probability of Connectivity (PC, Saura and Pascual-Hortal, 2007) to assess connectivity of the overall landscape, and ∆PC to assess the effect of various scenarios.

The *node* and *link importance* analyses remove each node and each link in turn, and calculate ∆PC to assess the importance of each node and each link to overall connectivity. The results of this analysis are presented in schematic "ball-and-stick" diagrams. They identify nodes and links that are important for landscape connectivity because they both contribute to overall connectivity and are non-redundant, such that their loss would greatly reduce overall landscape connectivity.

The *linkage* analysis assesses the effect on landscape connectivity of building a single wildlife passage structure at each contingent unit, representing stretches of roads and highways across Massachusetts. Contingent units that receive a high ∆PC represent places where a wildlife passage structure could greatly increase landscape connectivity. The effects of building multiple wildlife passage structures may be assessed by adding the ∆PCs for individual structures.

Selecting conservation nodes

Conservation nodes were built from a combination of areas including BioMap2 cores (Massachusetts Department of Fish & Game and The Nature Conservancy, 2010) and areas of permanently protected open space where the CAPS Index of Ecological Integrity (IEI; McGarigal et al., 2011) was ≥0.7. The goal was to include areas of high ecological value, while connecting them as much as feasible.

The procedure was as follows:

1. BioMap2 candidate forest cores were generalized to include streams and small nonforested patches that had been excluded. Because the final cores used in BioMap2 were a reduced set, we used the candidate cores (J. Dyson, TNC, pers. comm.).

2. BioMap2 candidate wetlands with IEI ≥ 0.5 were generalized to remove tiny wetlands and thin linear sections. As with forest cores, we used candidate wetlands (J. Dyson, TNC, pers. comm.).

3. Lentic portions of BioMap2 aquatic cores were included.

4. BioMap2 vernal pool complexes were included.

5. Permanently protected open space where IEI ≥ 0.7 was included. We generalized these areas to remove thin linear sections and small areas, include unpaved and zero-traffic roads, and connect nearly adjacent areas.

6. We took the union of all above layers.

7. We erased all areas where there were paved roads with nonzero traffic and railroads, with a one cell buffer to insure larger roads and railroads always subdivide nodes.

8. Small inclusions in nodes were dissolved away.

9. Finally, we applied a size threshold of 200 ha. This resulted in 405 nodes representing 17.2% of the landscape.

Selecting contingent units

In this analysis, contingent units represent stretches of roads and highways where wildlife passage structures could be built (though this approach can be applied to other types of contingent units, such as parcels that might be developed, thus interrupting regional connectivity). We used MassDOT 1:5000 roads layer (MassGIS). We selected all roads with mean daily traffic rates (ADT) ≥ 500 vehicles/day, to exclude smaller roads that are unlikely to have a significant effect on wildlife migration and dispersal at regional scales. We converted these roads to a 30 m grid, and delineated ca. 300 m segments. All segments that included road intersections were dropped, because passage structures are unlikely to be built over or under road intersections. This process yielded 45,746 contingent units, representing ca. 300 m long high-traffic road stretches where wildlife passage structures could potentially be built.

Landscape resistance

In this project (as in Critical Linkages I and the CAPS connectedness and aquatic connectedness metrics), we assess connectivity using the concept of landscape resistance. In a grid representation of the landscape, each cell has a value that represents how resistant that cell is to movement. Landscape resistance is often assigned for individual species or assemblages via expert knowledge, as empirical estimates are difficult to obtain. Resistant landscapes are commonly used in constructing least-cost paths between two points; they are also used for the resistant kernel algorithm we use in the CAPS connectedness metric and for assessing connectivity for wildlife species (Compton et al., 2007).

In CAPS, we assign landscape resistance uniquely for each focal cell based on the ecological distance from it to each neighboring cell. We measure ecological distance using a number of ecological settings variables (described in McGarigal et al., 2011, Appendix D). These 23 variables describe abiotic, vegetative, and anthropogenic aspects of the landscape, including, for example, growing season degree days, soil pH, wetness, vegetative structure, imperviousness, and traffic rate. Each of these settings variables has a value for each 30 m cell; together, they describe all important ecological aspects of each cell, to the extent possible with existing GIS data.

Because CAPS is a coarse-filter analysis, concerned with ecological communities rather than particular species, landscape resistance depends on the ecological setting of each cell; thus, there is a unique landscape resistance grid for each cell in the landscape. For each focal cell, we calculate ecological distance by taking the weighted Euclidean distance between the focal cell's location in settings space and the location of each other cell in the neighborhood in settings space (across 23 dimensions). Each settings variable is weighted to reflect its importance in determining landscape resistance (for weights, see McGarigal et al., 2011, Appendix G).

Random low-cost paths and conductance index

We assessed the functional distance between each pair of nodes using a new approach, random low-cost paths. It would be straightforward to connect one or more points in each node to one or more points in each neighboring node with a least-cost path; however, there are a number of drawbacks to using least-cost paths. They typically select unrealistically narrow corridors (e.g., one cell wide—something that would be unlikely to be used by most migrating or dispersing animals). As a result, least-cost paths are very sensitive to small GIS errors. They also ignore the number of alternatives, failing to distinguish between situations where there is a single path and situations where there are many alternatives. There are significant limits, therefore, to how usefully one can assess landscape connectivity with least-cost paths.

Our approach is to add some random variation to least-cost paths, making them sub-optimal and variable. We believe this approach, which we call random low-cost paths, more realistically represents the way animals move through the landscape, and more completely and robustly describes the connectivity between two areas. Random low-cost paths have three parameters: one that determines how random they are (ranging from deterministic least-cost paths to random walks), and two momentum parameters that determine the grain of randomness. For this project, we selected parameters that gave "reasonable" paths, as there is no direct biological interpretation of these parameters.

To assess the functional distance between each pair of nodes, we selected 1,000 random points within each node (the "from-node"). These random points were stratified by the representation of each group of ecological communities (Table 1) within the from-node. We then constructed a random low-cost path from each of these points to the first point in the same community group encountered in each neighboring node (the "to-node"). If a community group in the from-node doesn't exist in the to-node, that path is dropped. Paths are built in both directions between each pair of nodes. For each focal community (based on cells in the from-node), random low-cost paths are built on a resistant landscape based on cells in that community group in the to-node. This is done by following a resistant kernel built on a number of points in the to-node "uphill" from the from-node. The result is a set of up to 2,000 random low-cost paths between each nearby (≤10 km between centroids) pair of nodes in the landscape, stratified by ecological community. Stratification by ecological community insures that connections are made between similar cells, such that it is likely that an animal moving from one node to another would find habitat at its destination. Paths between each pair of points honor the landscape resistance for the community in the focal cell—thus, a path from a ridgetop cell will favor dry, steep ridgetops, whereas a path from a wetland will favor wetlands and low, wet areas.

Table 1. Grouped ecological communities used in building random low-cost paths.

Community group
Forest
Forested wetland
Non-forested wetlands
Water (lentic)
Water (lotic)
Open uplands
Coastal uplands
Salt marsh

We measured the functional length of each path by adding the landscape resistance (based on each starting point in the from-node) along the path's length. This gives functional distance, which integrates the distance traveled by the path in meters with the resistance of the intervening landscape given each cell's ecological distance from the starting cell to each cell along the path. The minimum resistance value is 1.0, so a 1 km long path through cells in an identical setting as the starting cell would have a functional distance of 1,000.

We converted these functional distances to probability of connection using a Gaussian density function based on a bandwidth representing dispersal ability. As this is a coarse-filter assessment, we are not focusing on individual species, thus, we used a series of bandwidths (2 km, 5 km, and 10 km) to represent a range of dispersal abilities. All further analyses involving probability of connection were repeated for each of these bandwidths, and results are supplied separately for each bandwidth. The probability for a path with a given functional distance at a given bandwidth represents the probability that an animal will be able to successfully traverse the path.

The first result of this analysis is the *Conductance Index*, which is simply a sum of all random low-cost paths in the landscape, each weighted by its probability and by the mean value of the two nodes (the sum of IEI for these nodes). The conductance index is a grid, where cells with higher values indicate a greater probability that animals will pass through these cells. A separate conductance index was created for each bandwidth.

Contingent units crossed by each path

When building random low-cost paths, we recorded the contingent units traversed by each path. For each traversed contingent unit, we recorded the decrease in functional distance (and thus increase in connectivity) resulting from the installation of a wildlife passage structure (assumed to result in a 90% reduction in the terrestrial barriers score and a 90% reduction in traffic, because some number of individuals avoid using passage structures). Although paths sometimes cross contingent units obliquely or zig-zag across a unit multiple times, we counted only one changed cell for each crossing of a contingent unit. These values are used in linkage analysis, below.

Link probability and translating to a graph

For each pair of nodes (in each direction), we took the mean of the 1,000 path probabilities to give a link probability. This represents the probability that animals in the from-node will be able to successfully traverse the landscape to the to-node.

At this point, we moved the data to a graph representation (Urban and Keitt, 2001). A graph consists of a number of *nodes*, connected by *links*. Each node may have a value, representing the size or value of the node. Each link may have a distance or probability, representing connections between pairs of nodes.

Conservation nodes became the graph nodes, where the value of each node was the sum of IEI across all cells in the node, integrating node area and ecological integrity. Graph links were represented by link probabilities, based on the mean functional probability of connectivity along 1,000 random low-cost paths. Link probabilities between pairs of nodes were asymmetrical, since the link probability need not be the same in both directions of movement. There was a separate graph for each bandwidth (2 km, 5 km, and 10 km), and all analyses were done in parallel for each bandwidth.

Probability of Connectivity (PC)

We used the probability of connectivity index, (PC, Saura and Pascual-Hortal, 2007) to assess connectivity of the landscape as a whole:

$$PC = \frac{\sum_{i=1}^{n}\sum_{j=1}^{n} a_i a_j p_{ij}^{*}}{A_L^2}$$

where n is the number of nodes, a_i and a_j are values of nodes i and j, p_{ij} are link probabilities between nodes i and j, A_L is the value of the full landscape, and p^{*}_{ij} is the maximum joint probability of all possible paths between nodes i and j.

PC is based on the size of habitat patches or conservation nodes and the probability of links between them in a graph framework. PC is defined as the probability that an animal in a random node would be able to traverse the network to any other given node in the landscape. Distant nodes are connected via stepping stones, and the probability of these connections is the maximum joint probability of links connecting the two nodes. PC gives a robust and meaningful measure of the connectivity of a landscape. It ranges from 1.0 for a landscape that occurs entirely within a single node, to near 0 for highly fragmented landscapes.

Two landscapes may be compared with ΔPC, (Saura and Pascual-Hortal, 2007), which is simply the different in PC between two landscapes. ΔPC may represent the difference between two actual landscapes, between a landscape at a current and future time, or between a landscape and a modification of the same landscape. In Critical Linkages II, we use ΔPC to assess node and link importance, as well as the effect of potential road crossing structures on regional landscape connectivity.

Node and link importance

Node importance was assessed by setting the value of each node to 0 in turn, recalculating PC, and subtracting this modified PC from PC for the original landscape, resulting in ΔPC for each node. These ΔPCs represent the loss in landscape connectivity that would result from the total loss of each node. We also applied a modified version of this process in which nodes all had the same value; this relative node importance represents the importance of each node based solely on position in the landscape, ignoring the size and ecological integrity of nodes.

Likewise, we assessed link importance by setting the link probability (in both directions) to 0 for each link in turn, and calculating ∆PC for each link. These ∆PCs represent the importance of each link for landscape connectivity. Link importance is affected by both the link probability of each link and the redundancy of links. Links with a high link probability that connect high-value nodes will have a high importance if they are irreplaceable (i.e., there are no alternatives to connect these nodes).

Node and link importance were assessed at each of the bandwidths: 2, 5, and 10 km.

Linkage analysis

The core of the Critical Linkages II analysis is the assessment of the potential contribution of wildlife passage structures (contingent units) to regional connectivity. This is done separately for each contingent unit.

We assessed individual contingent units by iterating through all units. For each unit, we modified the functional distance for all paths that traverse that unit (as described under *Contingent units crossed by each path*, above) to simulate the installation of a wildlife passage structure at that unit. We then recalculated link probabilities and PC, and calculated ∆PC from the original landscape, yielding the increase in landscape-wide connectivity to be gained from the installation of a wildlife passage structure at this location. Results for all contingent units were mapped, and the units with the largest ∆PC are listed in a table.

We also assessed the joint effect of constructing multiple neighboring wildlife passage structures simultaneously by randomly changing multiple nearby structures and calculating a joint ∆PC. For this wildlife passage analysis, summed ∆PCs are a very close approximation of joint ∆PCs (unpublished analysis). Thus, to assess the effects of installing multiple wildlife passage structures, the ∆PCs for all individual structures may be summed.

Results

Our node selection procedure resulted in 405 conservation nodes ranging in area from 200 to 24,866 ha, making up 17.2% of Massachusetts (Fig. 1). The majority of nodes fell in the less-developed western half of the state, as did most large nodes. In several parts of western Massachusetts, many nodes are adjacent to each other, separated only by roads.

Statewide, there were 45,746 contingent units representing approximately 300 m stretches of roads with mean daily traffic ≥ 500 vehicles/day. Figure 2 shows contingent units along major roads in a sample area. Note that units that fell on road intersections were omitted to avoid giving scores to unrealistic crossings at the intersections of two roads.

Figure 3 shows sample random low-cost paths at a bandwidth of 10 km (all results presented here are for 10 km). All paths between each pair of nearby nodes (1,000 in each direction) are weighted by path probability and node value and superimposed to give the conductance index (Fig. 4). Conductance highlights areas of high flow among conservation nodes at a fine scale.

Coarser scale connectivity among nodes is better assessed with link probabilities (Fig. 5). The sizes of circles at node centroids indicate the node value (sum of IEI for each node), while the width of connecting lines indicates the link probabilities between each pair of nodes. This figure, in a graph framework, is schematic, and does not indicate the extent of nodes or the actual paths of flow. Note that in the eastern half of Massachusetts, nodes fall into small groups, disconnected from the main network that interconnects nearly all of the western Massachusetts nodes (at a bandwidth of 10 km, our largest). Many of these eastern Massachusetts nodes form their own small to medium clusters. Note also that there are few links connecting across the Connecticut River valley in the western third of the state. This is also true, to a lesser extent, of the Housatonic valley.

The importance of each node and link is assessed by an importance analysis (Fig. 6). Here, the size of nodes and width of links indicates the loss in regional connectivity that would result if the corresponding node or link was removed from the network. Some low-value nodes may provide important connectors and thus have high importance. Likewise, high-value nodes may not be particularly important for connectivity in the network, either because they are relatively isolated (e.g., they act as a cul-de-sac), or because nearby redundant nodes can replace their connectivity if they are removed. The same is true for links: in particular, many high-probability links are of low importance, because they do not form a part of the minimum spanning tree, which represents the shortest interconnections among nodes. Note that the central node that represents the Quabbin Reservoir and surrounding forest land is both a high-value node (Fig. 5b) and of high importance, acting as a hub for several important links (Fig. 6b). This reflects both its size and ecological integrity, and its central location in the region.

The linkage analysis (Fig. 7) gives the ΔPC that would result from building a road passage structure at each contingent unit, one at a time. Most contingent units would contribute little to regional connectivity, while a few units contribute disproportionately (Fig. 8). The 10 linkages with the largest ΔPC contribute 9.5% of the total ΔPC obtainable if road passages were installed at all 45,746 units, and the top 20 linkages contribute 16.4% of total ΔPC. Thus, installing a small number of road passage structures in strategic locations could result in a large improvement in regional connectivity. The top 20 linkages statewide (Fig. 9) fall into four groups: on the Mass Pike and Route 20 between Beartown and October Mountain State Forests (Fig. 10), on the Mass Pike at the western edge of Blandford (Fig. 11), on Route 202 northwest of the

Quabbin (Fig. 12), and on Route 2 at the western edge of Orange (Fig. 13). The combined effect of constructing multiple nearby road passage structures may be assessed by summing the ΔPCs of individual structures.

All GIS data are available for downloading. See Appendix A.

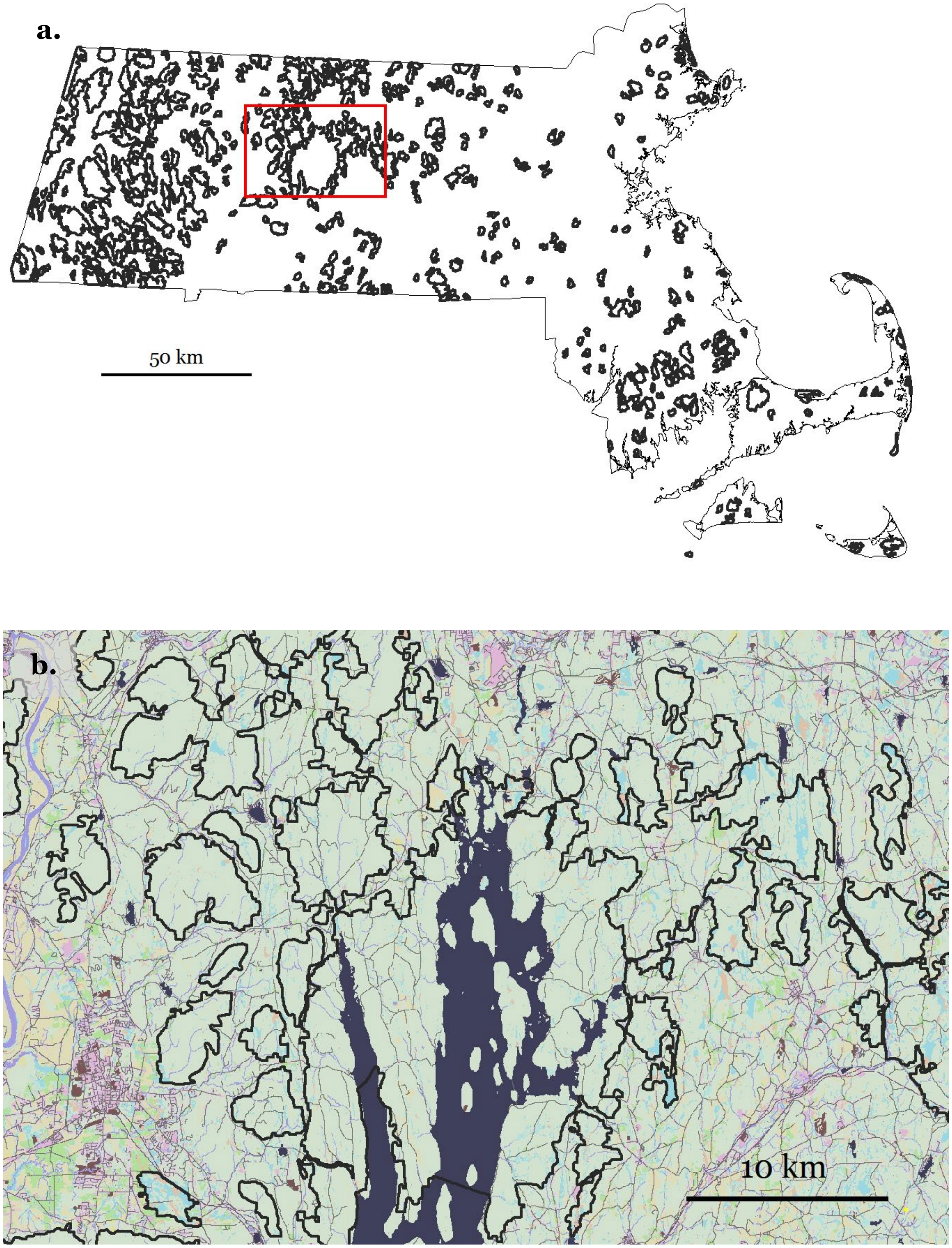

Figure 1. Conservation nodes (dark gray outlines). (a) statewide (with focal area outlined in red), and (b) focal area, showing nodes outlined over CAPS landcover. These nodes represent the proposed reserve network used in this analysis.

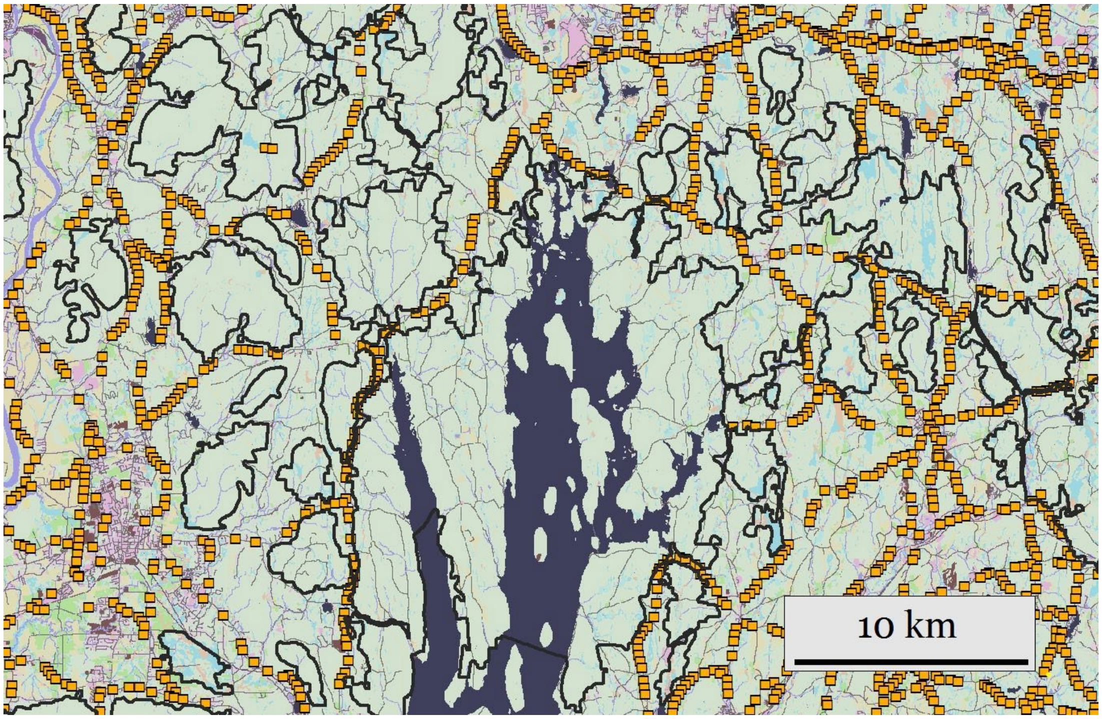

Figure 2. Contingent units, focal area. Contingent units are ca. 300 m segments of roads (with ≥ 500 vehicles/day), excluding road intersections.

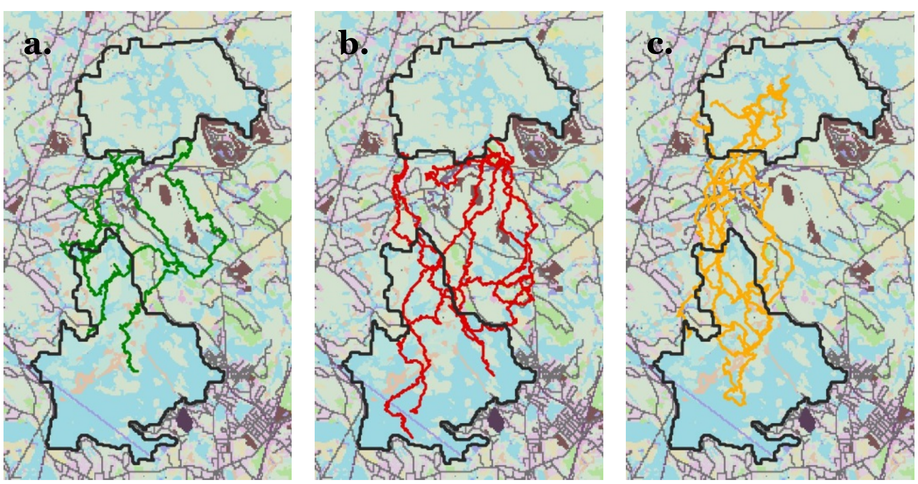

Figure 3. Examples of random low-cost paths for three community groups (a) forest, (b) forested wetland, and (c) shrub swamp. All paths originate in a random cell of the corresponding community group in the southern node, following a low-cost path to the first cell in the same community group in the northern node. Paths for different community groups are low-cost for their community, thus, for example, wetland paths tend to traverse wet areas.

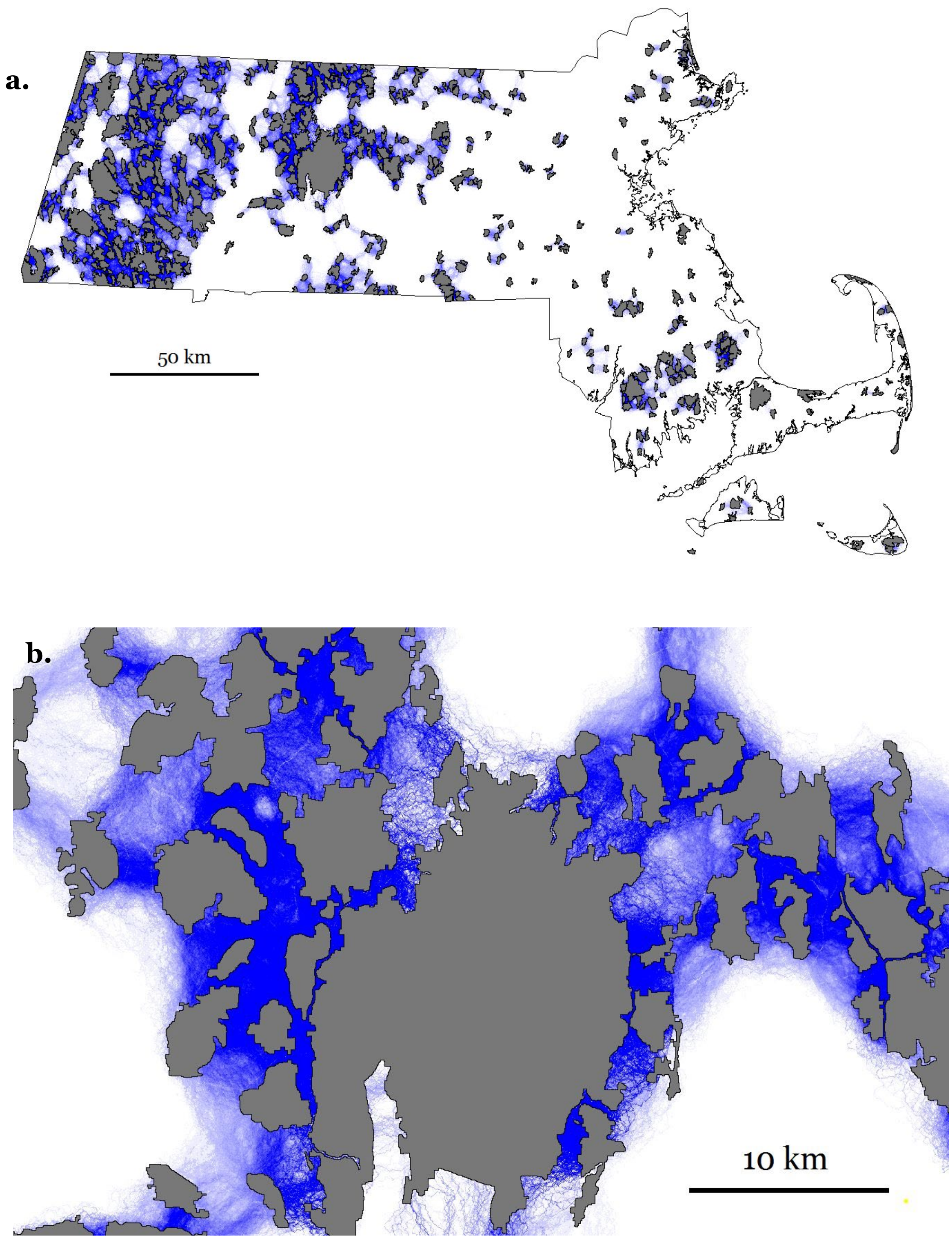

Figure 4. Conductance at 10 km bandwidth (blue) and conservation nodes (gray). (a) statewide, and (b) focal area. Conductance indicates the paths between nodes at a fine scale.

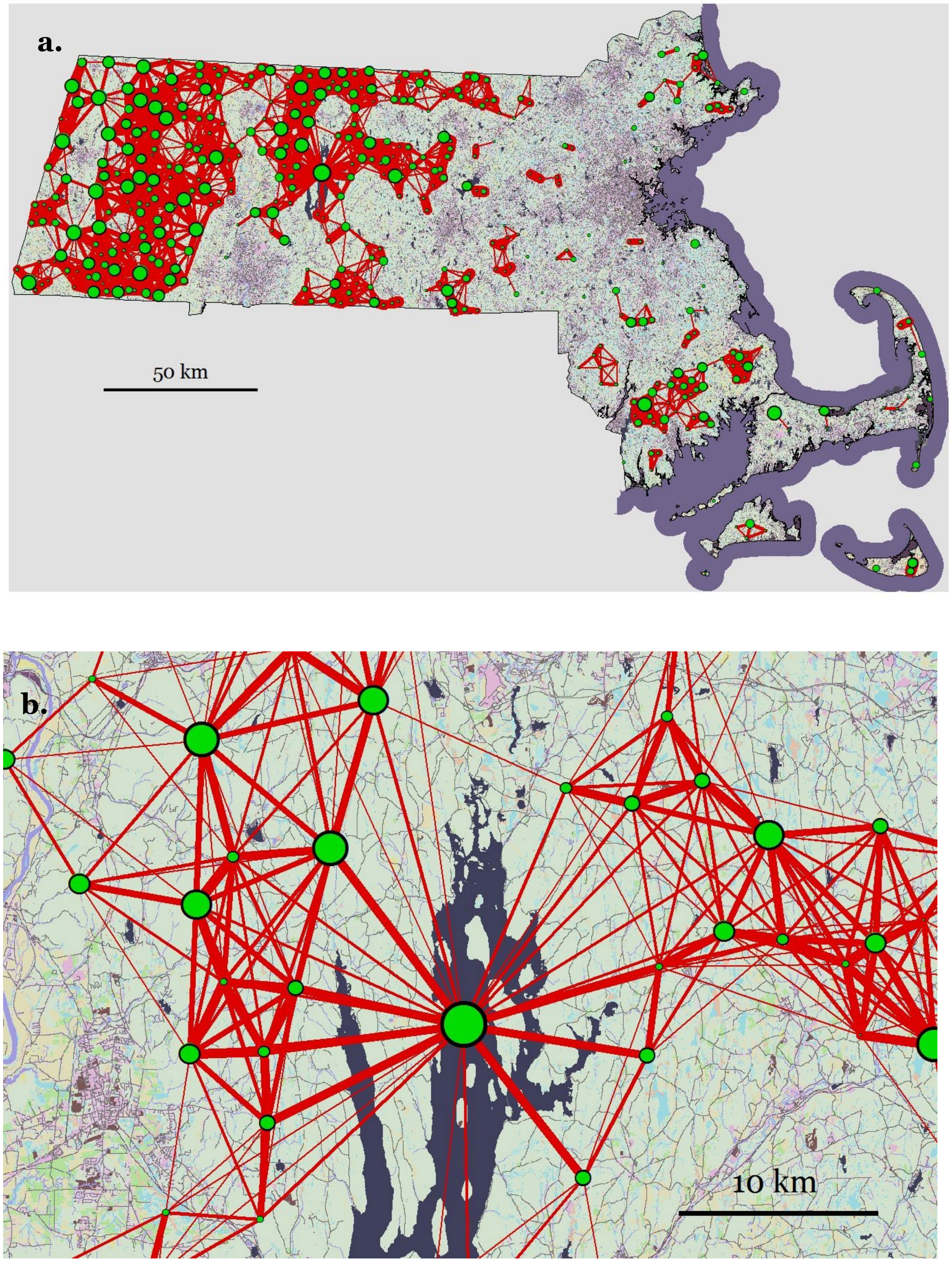

Figure 5. Node values (green circles) and link probabilities (red lines) at a bandwidth of 10 km, (a) statewide, and (b) focal area. The size of circles representing node values (ΣIEI) indicate the size and integrity of nodes. The width of lines representing link probabilities indicate the mean probability of connection between pairs of nodes. Nodes and links are schematic and do not indicate actual node boundaries nor link paths.

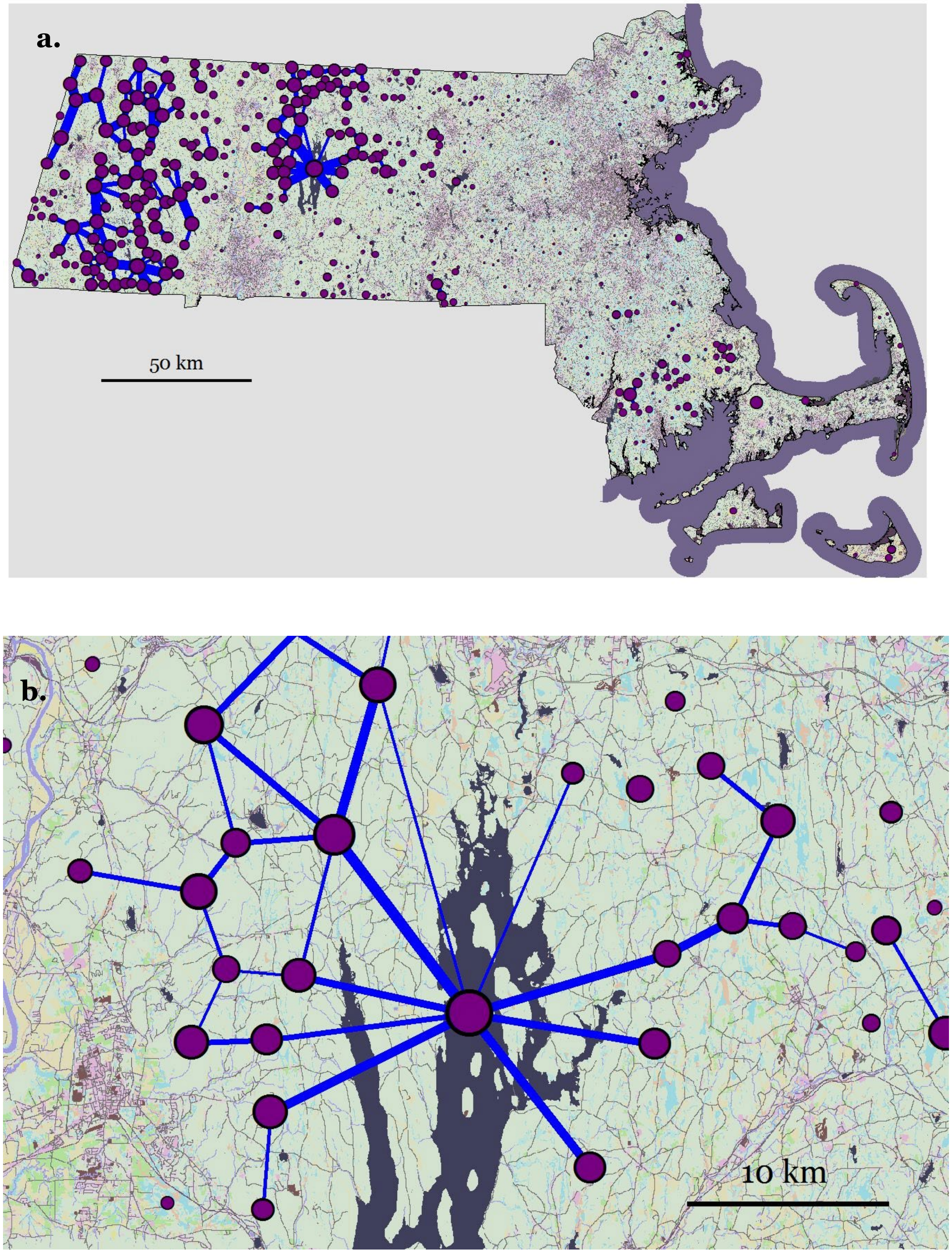

Figure 6. Node importance (purple circles) and link importance (blue lines) at a bandwidth of 10 km, (a) statewide, and (b) focal area. Importance of nodes and links is the loss in regional connectivity that would occur if the node or link were removed. Nodes and links are schematic and do not indicate actual node boundaries nor link paths.

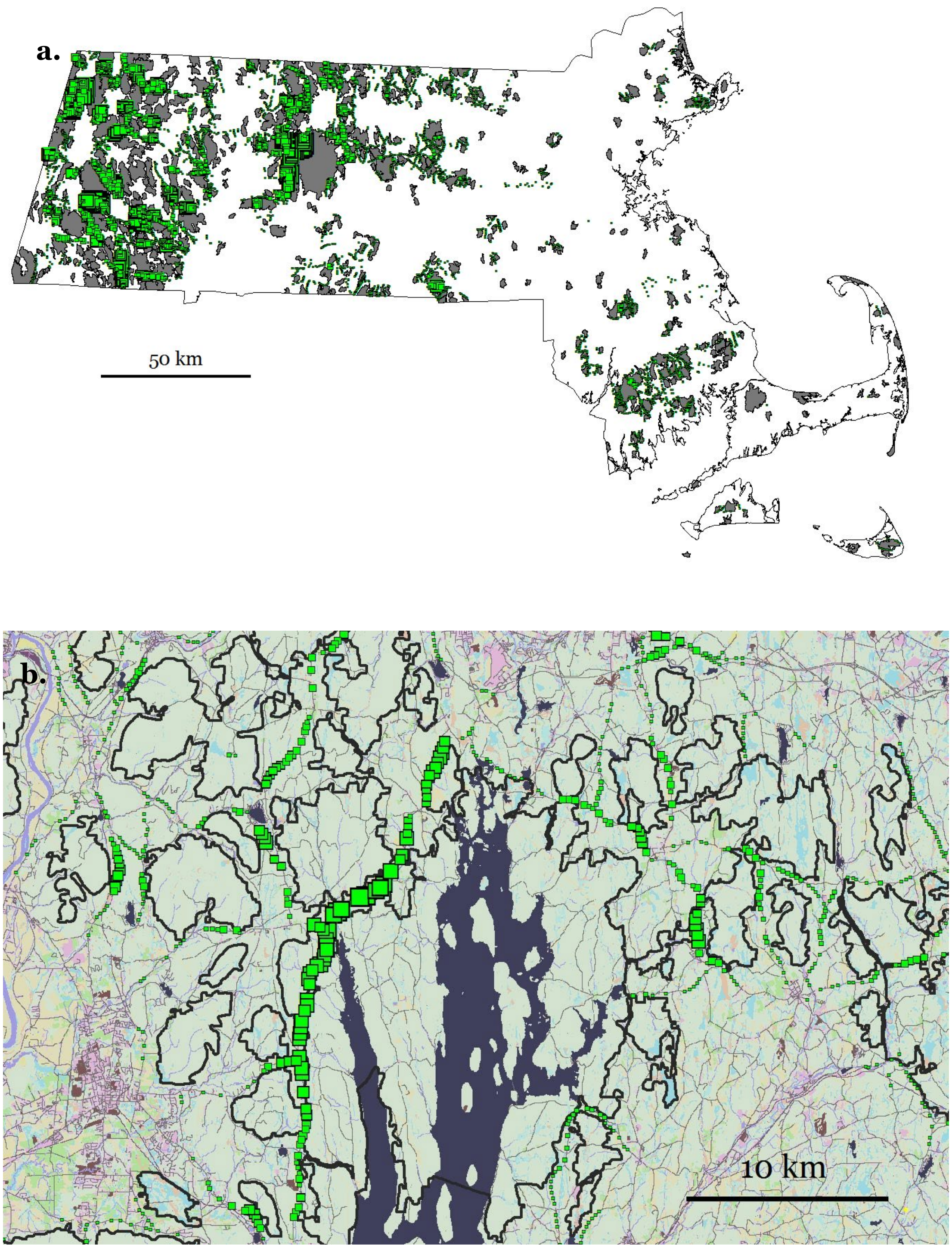

Figure 7. Linkages (green squares) and nodes, (a) statewide, and (b) focal area. The size of the squares indicates the ΔPC resulting from installing a road passages structure at each contingent unit. High-valued units indicate places where a road passage structure is expected to make a large contribution to regional connectivity.

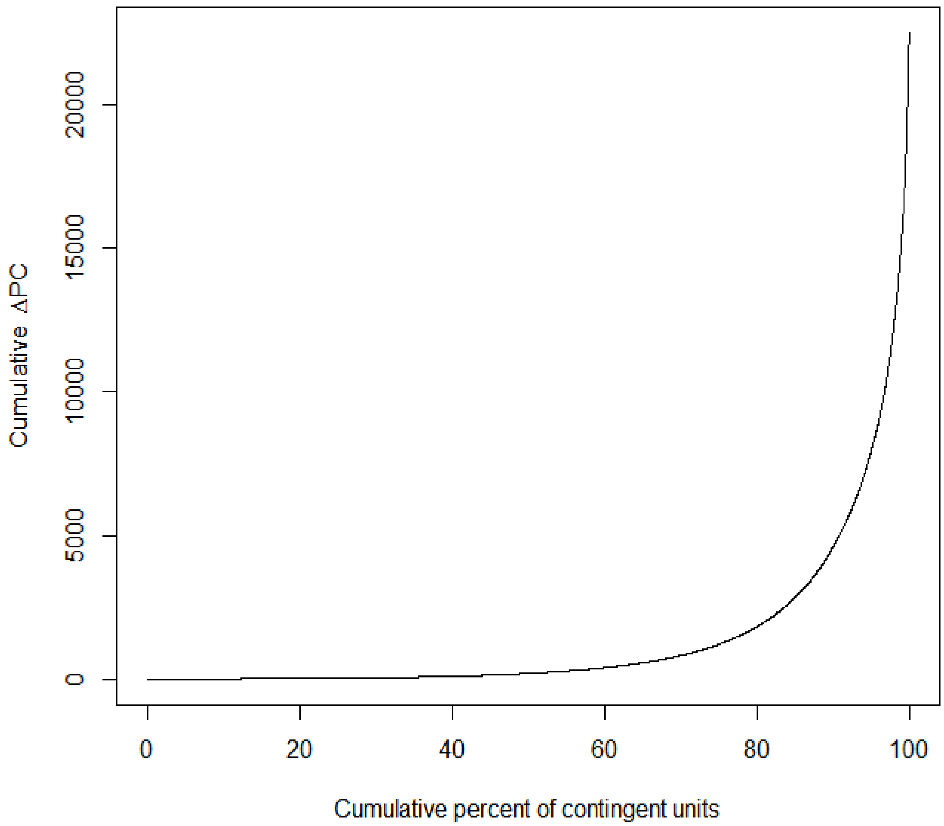

Figure 8. Cumulative ΔPC from contingent units in linkages analysis. This graph indicates that most contingent units would contribute little to regional connectivity, while a small percent of units have great leverage.

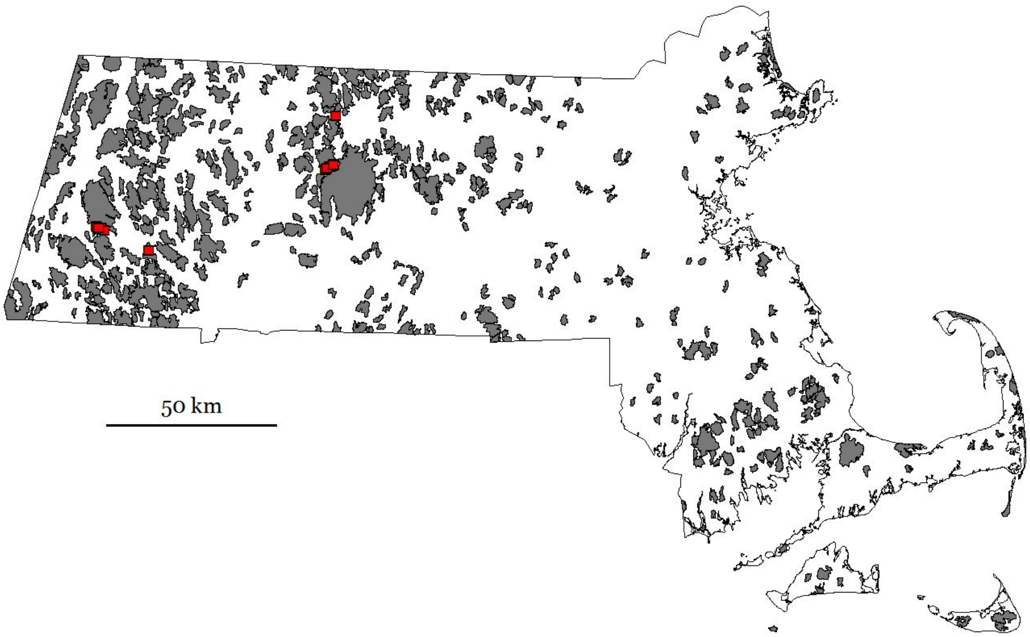

Fig. 9. Best 20 linkages statewide (red).

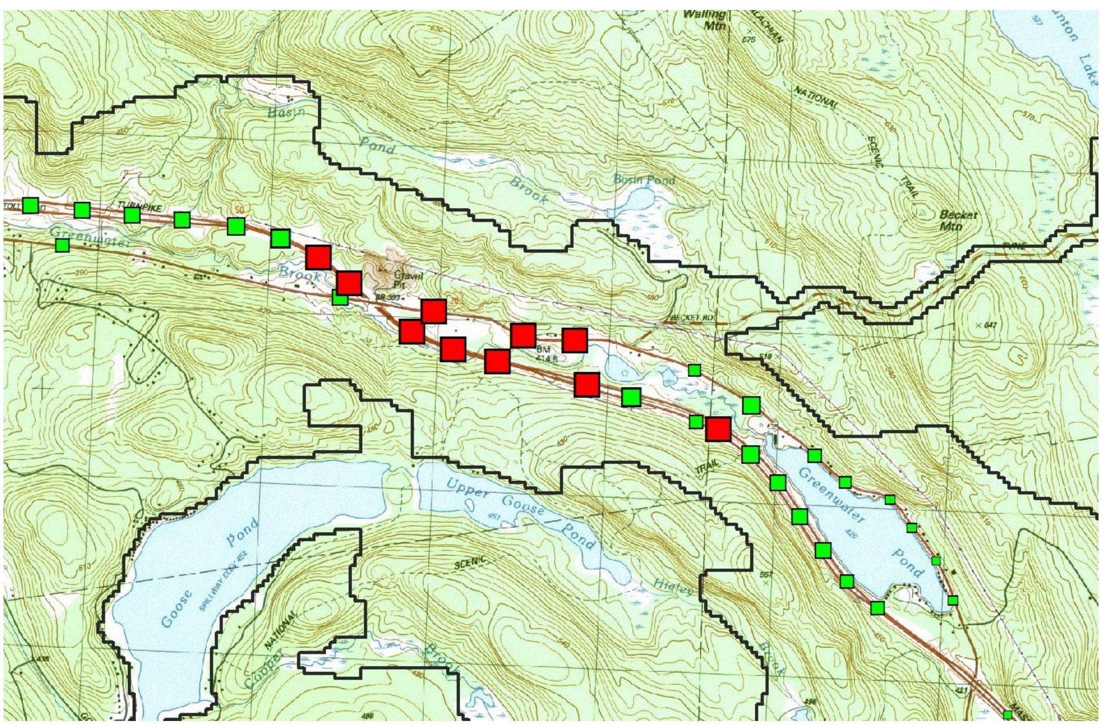

Fig. 10. Best statewide linkages (red) and other linkages (green) that occur on the Mass Pike and Route 20 between Beartown and October Mountain State Forests.

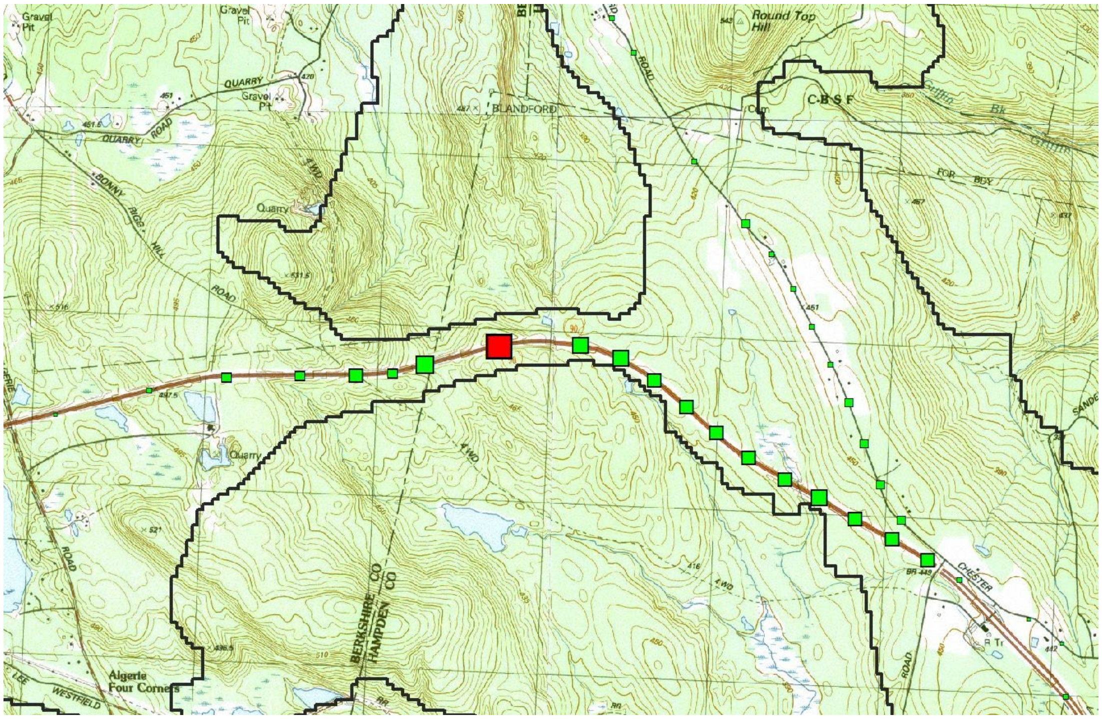

Fig. 11. Best statewide linkages (red) and other linkages (green) that occur on the Mass Pike at the west edge of Blandford

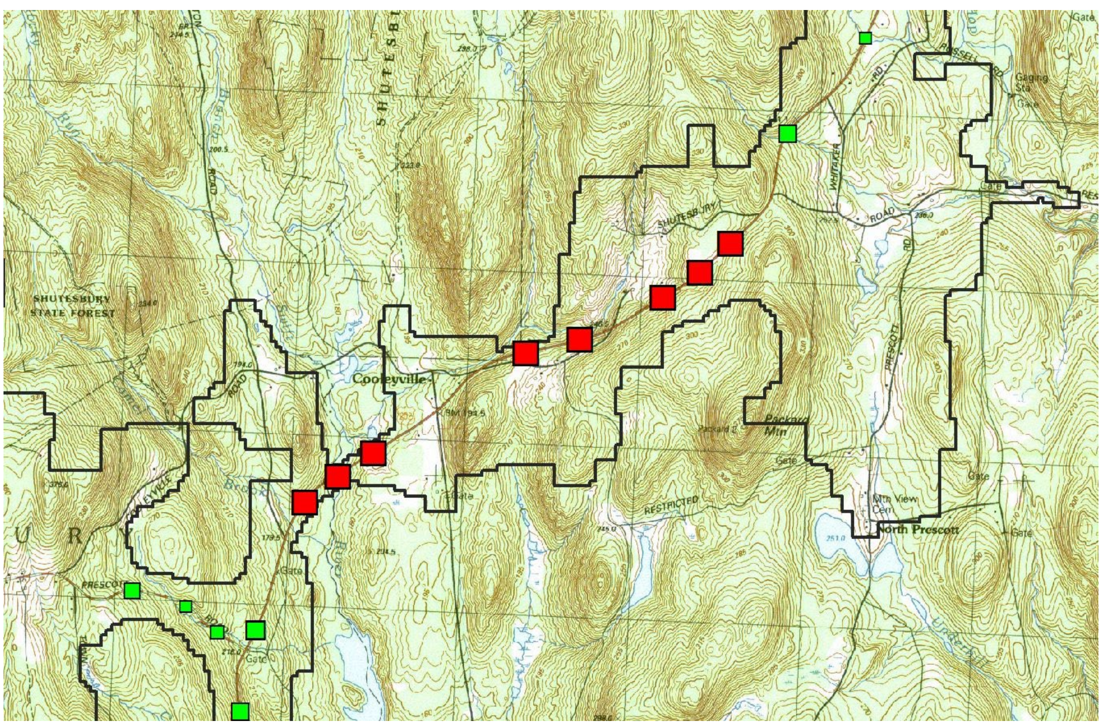

Fig. 12. Best statewide linkages (red) and other linkages (green) that on Route 202 northwest of the Quabbin.

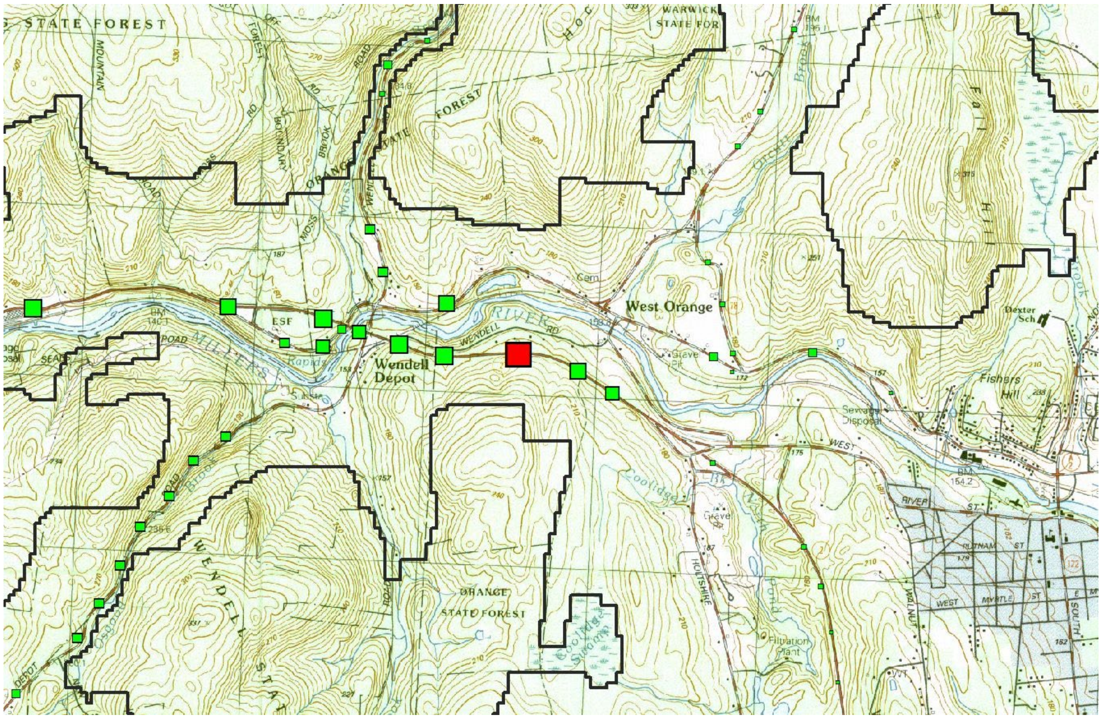

Fig. 13. Best statewide linkages (red) and other linkages (green) that occur on Route 2 at the west edge of Orange.

Discussion

Given the importance of regional connectivity for wildlife conservation, especially during a time of rapid climate change, the significant barrier effects of roads, and the expense of installing effective road passage structures, a strategic approach to locating such structures is necessary. Critical Linkages II provides a framework for assessing the effects on regional connectivity of installing road passage structures at each potential location. This analysis integrates information on ecological communities, roads, road traffic, and development, and arrangement of conservation nodes. Results include information on the value and importance of nodes and generalized links among them, maps of fine-scale conductance, and a valuation of all road segments for their potential as wildlife passage structures. A small number of road segments account for a large proportion of potential increase in regional connectivity, suggesting the payoff for a strategic approach could be large.

Critical Linkages I focused on potential increases in local connectivity for three types of infrastructure upgrades: culvert upgrades, dam removal, and wildlife passage structures. Culverts and dams affect connectivity for aquatic organisms (fish and non-flying aquatic invertebrates) via the stream network, whereas wildlife passage structures affect terrestrial and semi-terrestrial wildlife (amphibians, reptiles, mammals, nonmigratory birds, and possibly some invertebrates). Because of the linear nature of stream networks, increasing regional aquatic connectivity is a matter of sequentially increasing local connectivity. Increasing terrestrial connectivity, on the other hand, requires a different, regional approach, such as was implemented in Critical Linkages II. At the same time, the high cost of effective wildlife passage structures suggests that structures should generally be located based on regional, rather than local connectivity. Thus, Critical Linkages II can best be thought of as a complement to Critical Linkages I's analyses for culverts and dams, and a replacement for its analysis of wildlife passage structures when the goal is increasing regional connectivity.

It is important to note that Critical Linkages II assumes that wildlife passage structures will be constructed in ways that will be effective for the wildlife species for which they are targeted. Wildlife passage structures that look good on paper may be ineffective due to inadequate size, excessive length, insufficient lighting, inappropriate substrate, approaches that fail to funnel wildlife, and locations in inappropriate habitat (Jackson and Griffin 2000). An equally important issue, too often ignored, is the fencing or barrier system used to prevent animals from crossing roads near structures rather than using the structures themselves. Long-term maintenance of wildlife passage structures and associated barriers is also important to ensure they continue to function over the long term. Design of wildlife passage structures is an ongoing area of research (Clevenger and Huijser 2011). In this analysis, we assume that structures will be designed, constructed, and maintained appropriately.

An assumption of this analysis, inherent in the way low-cost paths are modified for the installation of wildlife passage structures, is that wildlife passage structures do not attract animals, nor are fences long enough (e.g., kilometers) to funnel wildlife long distances to reach passages. In places where several units with high ∆PC occur along a road, it may be possible to increase the gain in connectivity by constructing several passage structures. It might also be possible in some locations to achieve a greater gain by constructing long funneling fences. These are site- and species-specific issues not addressed by this landscape analysis.

As with any GIS-based landscape analysis, errors in GIS data are likely to lead to errors in results. In particular, errors in road traffic data will affect this analysis, though such errors tend to be less of an issue with high-traffic roads (which have the most leverage in this analysis), where traffic rates are often measured directly rather than interpolated. Although GIS errors can have a large effect on landscape resistance, the use of random low-cost paths makes this analysis relatively robust to scattered GIS errors.

Because this analysis looks at regional connectivity over large distances, it could usefully be done across even larger regions, such as New England or the entire northeast. Even when conservation is practiced at local or state scales (e.g., by state agencies), a multi-state regional perspective is important.

This analysis is a coarse-filter, ecosystem based approach. It was done at three different bandwidths to represent a variety of dispersal distances, but is not otherwise tuned to individual species. The same approach could be easily applied to particular species by tuning the bandwidth to the species' dispersal abilities, using species-specific landscape resistances, and basing nodes and focal communities on habitat for the selected species.

Although we have not yet implemented it, we envision a related regional analysis in which contingent units represent parcels, rather than road segments. In such an analysis, the focus would be on the loss in regional connectivity due to parcels being developed. Such an analysis would highlight parcels that, though they may be of low ecological integrity in themselves, contribute greatly to regional connectivity, such that protecting them from development should be a conservation priority.

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Glossary

Conductance. The degree to which a focal spatial unit (grid cell) impedes or facilitates ecological flows between other spatial units; in other words, to what extent does a focal cell play a role in connectivity between point A and point B, or to what degree does a focal cell function as a thruway for flows between point A and point B. Conductance measures the degree to which a focal cell functions as a linkage; it integrates the irreplaceability of the point (whether there are adequate alternative paths), and the ecological flow through that point, which depends on the size and proximity of nearby nodes, as well as intervening **landscape resistance**. Conductance is applied to a particular landscape "as is," without assessing contingent effects on connectivity, as is done in a **critical linkage** analysis.

Conservation node (node). A generic term for a contiguous area of conservation interest; the regional connectivity analysis assesses connectivity among nodes. Nodes are typically heterogeneous in ecological setting, and they correspond to mapped area of the landscape (they are not merely abstract points).

Contingent units ("units" for short). Areas (defined either automatically or by the user) where landscape resistance may change in the future (e.g., parcels of land that may be developed, or roads that may be mitigated by passage structures). These are the elements evaluated in a **critical linkage** analysis.

Critical linkage. A **unit** that has great leverage on connectivity, such as a parcel (or set of parcels, not necessarily contiguous) that would seriously disrupt connectivity if developed. A critical linkage analysis assesses the relative importance of many units (and combinations of units) for connectivity.

Ecological distance. Distance between two points in **ecological setting** space. This is an aspatial concept.

Ecological settings. Variables corresponding to each point in the landscape that defines the natural community of that point (e.g., elevation, temperature, solar gain, wetness, flow velocity, lithology). In the 2011 version of CAPS, each point is defined by 23 settings variables.

Functional distance. Distance between two points on a map, taking into account landscape resistance. This is dependent on an integration of the physical distance between the points and the **ecological distance** between the starting point and each intervening point along the a particular path, typically either the **least-cost path** or a **random low-cost path**.

Landscape continuity. Refers to the physical continuity or structural connectedness of the landscape.

Landscape connectivity. Refers to the functional connectedness of the landscape as perceived by one or more focal organisms or focal ecological process; that is, the ability of the landscape to facilitate or impede relevant ecological flows. Landscape connectivity reflects the interaction of ecological flows (e.g., movement of organisms) with the physical landscape structure (i.e., the composition and spatial configuration of the landscape).

Landscape resistance. The **ecological distance** between a focal cell and other cells in the landscape.

Least-cost path. The shortest path through a **resistant landscape** between two points. The least-cost path between a focal cell and any other point in the landscape is encoded in a **resistant kernel**.

Local connectivity. The spatial scale at which the dominant organisms interact directly with the landscape via demographic processes such as home range movements and dispersal. This is the landscape context that an individual organism might experience during its lifetime.

Probability of Connectivity (PC). The probability that an animal in a random node would be able to traverse the network to any other given node in the landscape (Saura and Pascual-Hortal, 2007). PC measures regional connectivity through a network of nodes and links. It ranges from near 0 (tiny disconnected nodes) to 1.0 (a single fully connected node filling the landscape). PC may be compared between two landscapes, resulting in **ΔPC**, which measures the improvement (positive ΔPC) or loss (negative ΔPC) in regional connectivity given changes in the landscape. In Critical Linkages II, ΔPC is the measure of node and link importance, and of the value of each potential wildlife passage structure at a contingent unit.

Random low-cost path (RLCP). A stochastic version of the **least-cost path** that randomizes steps up the **resistant kernel**. The resulting path is expected to be of (reasonably) low cost, but not optimal. RLCP parameters determine how much the path can be expected to deviate from optimal; by default the directional probability at each step is proportional to the value of the resistant kernel in each direction. Typically many RLCPs are produced to assess the robustness of connectivity between two nodes, and to allow for critical linkage analysis.

Regional connectivity. The spatial scale exceeding that in which organisms directly interact with the landscape, measured by **Probability of Connectivity (PC)**. This is the scale at which long-term ecological processes such as range expansion/contraction and gene flow occur. At this scale, individuals generally do not interact with the landscape, but their offspring or their genes might.

Resistant kernel. A modification of the classic kernel estimator applied to a **resistant landscape** (where resistance is based on ecological distance). Refers either to a kernel applied to a single point, or the sum of kernels applied to multiple points in a landscape.

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Appendix A: Critical Linkages II results

Data organization. Critical Linkages results are available for download. This section lists the results and provides links. Data are available in grouped .zip files, listed below.

Data formats. Results from Critical Linkages II are supplied as shapefiles and grids. Grid results are supplied in two formats: Arc Grids and geoTIFFS. The coordinate reference system for all data is Massachusetts Mainland State Plane, NAD83.

Results. Each of the shapefiles and grids are listed below, with a description of the fields in each shapefile or values in each grid.

nodes (polygon shapefile). Contains a polygon delineating each conservation node.

ha	Size of node, in ha
iei	ΣIEI for the node

nodeimportance (point shapefile). Nodes represented by points, with node importance values at each bandwidth. There are two versions of node importance: absolute (where both node position and node value based on ΣIEI, are taken into account) and relative (where only node position is taken into account).

name	Name of node, based on protected open space or town name
iei	ΣIEI for the node
import2k	Node importance at a bandwidth of 2 km
import5k	Node importance at 5 km
import10k	Node importance at 10 km
relimport2k	Relative node importance (position but not size) at 2 km
relimport5k	Relative node importance at 5 km
relimport10k	Relative node importance at 10 km

linkimportance (line shapefile). Lines representing links between pairs of nodes. Link probability (both direct and via stepping stones) and link importance are supplied at each bandwidth.

P2k	Direct link probability at a bandwidth of 2 km
P5k	Direct link probability at 5 km
P10k	Direct link probability at 10 km
Ps2k	Link probability using stepping stones at a bandwidth of 2 km
Ps5k	Link probability using stepping stones at 5 km
Ps10k	Link probability using stepping stones at 10 km
import2k	Link importance at a bandwidth of 2 km
import5k	Link importance at 5 km
import10k	Link importance at 10 km

units (grid). Grid cells representing each contingent unit (potential wildlife crossing structure).

unit	The internal unit number for each road segment (corresponds to unit in *linkages*). In the geoTIFF version, values are arbitrary integers.

conduct2k, ***conduct5k***, ***conduct10k*** (grids). These grids contain the conductance index at each cell for a given bandwidth. The conductance index represents the link probability at each point scaled by node value. Note that conductance within from-node and to-node is 0; thus any nonzero conductance within a node is from paths passing through.

conductance	Value representing the conductance at each cell

linkages (point shapefile). Points representing potential road passage structures (contingent units). Each unit has a value for ΔPC at each bandwidth, representing varying dispersal distances. Links for which all ΔPC = 0 are excluded.

unit	Unit number (corresponds to the units grid)
delta2k	ΔPC for this unit at a bandwidth of 2 km
delta5k	ΔPC at 5 km
delta10k	ΔPC at 10 km

Downloads. All data are available via the links listed below. As the conductance grids are rather large, a separate download excluding them ("shapefiles") is available.

All data. All results from Critical Linkages II.

Shapefiles and geoTIFFs (11.3 MB).
https://landeco.umass.edu/web/CLII2013/shapetiffs.zip
Shapefiles and Arc grids (119 MB).
https://landeco.umass.edu/web/CLII2013/shapegrids.zip

Shapefiles only. All shapefile results. (1.1 MB).
https://landeco.umass.edu/web/CLII2013/shapefiles.zip

Grids only. All conductance grids and the units grid.

geoTIFFs (10.2 MB).
https://landeco.umass.edu/web/CLII2013/tiffs.zip
Arc grids (117 MB).
https://landeco.umass.edu/web/CLII2013/grids.zip