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Connectivity of core habitat in the Northeastern United States: Parks and protected areas in a landscape context

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A B S T R A C T

The exurbanization process, particularly rural residential development, is reducing the amount of roadless areas and remote habitat across the nation, with implications for biodiversity and ecosystem integrity of parks and protected areas. The need for connecting protected areas via existing habitat centers, or relatively undisturbed core areas, is greater than ever as exurbanization expands. Our objective was to make use of nationally available data sets on roads as well as information derived from satellite imagery, including impervious cover of the built environment and forest canopy density, to identify core habitat of the northeastern and mid-Atlantic USA. The identified core habitat areas, which covered 73,730 km^2 across 1177 discrete units, were stratified in terms of land ownership and management, and then analyzed in a landscape context using connectivity metrics derived from graph theory. The connectivity analysis made use of a suitability surface, derived from the land cover information, which approximated the costs incurred by hypothetical animals traversing the landscape. We show that protected areas are frequently identified as core habitat but are typically isolated, albeit sometimes buffered by adjacent multi-use lands (such as state or national forests). Over one third of the core habitat we identified has no protection, and another 42% is subject to motorized recreation or timber extraction. We provide maps showing the relative importance of core habitat areas for potentially connecting existing protected areas, and also provide an example of the vulnerability of connectivity to projected future residential development around one greater park ecosystem.

1. Introduction

Because ecological processes and species movements often span parks and protected area boundaries, it is necessary to evaluate current reserve networks in relation to surrounding unprotected habitat. The connectivity of habitat areas increases the effective size of existing protected areas and plays a critical role in species persistence, thus it has long been known that loss of connectivity can lead to localized extinctions (Carroll et al., 2004; Tilman et al., 1994). Connectivity of core habitat areas, i.e. those locations that are well buffered from the influence of human disturbance such as roads and associated development, is also important in the context stream biotic health (e.g. Goetz & Fiske, 2008) and species responses to climate change, with dispersal pathways between suitable habitat areas necessary to ensure species viability on longer time scales (Hannah et al., 2002). Due to the pace of landscape change in many areas, it is important to include characteristics of the intervening matrix when assessing functional connectivity and designing reserve networks (Calabrese & Fagan, 2004; Rothley & Rae, 2005). Moreover, in order to assess the potential for remaining roadless areas to augment current conservation networks and gauge their role in enhancing effective reserve size, it is necessary to determine the extent, configuration and management status as well (e.g. Hansen & DeFries, 2007).

Habitat loss and fragmentation resulting from residential development are widely known to impact the effectiveness of reserves and various aspects of biological diversity (Hansen et al., 2005). Low-density residential development has increased rapidly in the United States and is now the dominant development pattern in the United States, occupying over one million km^2 as of 2000 (Brown et al., 2005; Theobald, 2001). Nearly 40% of all housing units are contained in areas typified by low density development in a matrix of natural land cover types, i.e. the wildland–urban interface (Radeloff et al., 2005). The road building that accompanies development is a major contributor to habitat fragmentation and degradation. Roads present barriers to wildlife movement, are a direct cause of mortality to wildlife, and act to increase introductions of non-native species (Fahrig et al., 1995; Forman & Alexander, 1998; Gibbs & Shriver, 2002; Mader, 1984). Conversely, roadless areas have higher levels of native diversity and fewer invasive species (Glennon & Porter, 2005). As development continues, we can expect core habitat areas to decrease in size, number,

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and quality. As a result, they will be ever more difficult to protect in a natural state, particularly in historically more developed regions like the northeastern United States.

Our objectives here were to make use of remotely sensed and other spatial data sets in the eastern U.S. to identify core habitat areas, assess their landscape configuration, and identify their current management status. A related objective was to analyze the contribution of core areas to landscape connectivity across the study area using a graph theoretic approach, and assess the current set of protected areas in this region in a landscape context.

2. Data sets

2.1. Parks and protected areas

We used version 4 of the Protected Areas Database (DellaSala et al., 2001), consisting primarily of state level Gap Analysis Program (GAP) stewardship data compiled by the Conservation Biology Institute and the World Wildlife Fund, which classifies land into one of four broad stewardship categories based on the level of protection, particular ownership or management regimes that afford biological resources (Scott et al., 1993). Categories 1 and 2 lands are protected from conversion and are generally managed for maintenance of biological diversity. Examples of these include National Parks, State Parks, and designated Wilderness Areas. Category 3 includes lands that are protected from conversion, such as National Recreation Areas and National Scenic River segments, but also lands that may be subject to use that modifies habitat quality such as logging (most Forest Service lands fall into this category). Category 4 lands are afforded no formal protections, except for some county and municipal parks, with most lands in this category identified as private industrial forest lands and utility corporation lands. Finally, we used a 1:1,000,000, U.S. National Atlas Water Feature data set of rivers, streams, and lakes (ESRI, 2004a) to account for these areas in our analyses.

2.2. Vegetation cover

Tree cover information for the study area was obtained from a global, 500 m (0.25 km^2) resolution, continuous-fields tree cover map derived from the Moderate Resolution Imaging Spectroradiometer (MODIS) imagery. The map consists of continuous values indicating the fraction of each 500 m pixel covered by trees (i.e. canopy density). The year 2001 tree cover product was generated using a total of 68 phenological metrics derived from 40-day composites of shortwave visible and infrared (bands 1–7) imagery and band ratios that emphasize vegetation density (Hansen et al., 2003). Forest cover was estimated using these metrics and a regression tree algorithm trained with field data and Landsat forest class maps. Validation of the tree cover product indicates a standard misclassification error estimate of 11.5% (Hansen et al., 2002). At the time of this analysis the National Land Cover Database (NLCD) maps of tree cover, derived at finer resolution, were not yet available and, to date, have not been validated with field measurements. These data would be useful for future finer-scale analyses, particularly at the local level (Goetz, 2006).

2.3. The built environment

We made use of a roads data set, based on 1:100,000 United States Census Bureau TIGER 2000 line files, which can be found on the Environmental Systems Research Institute (ESRI) Data & Maps data disc supplied with ArcGIS software. Road classifications were updated by ESRI using reference data supplied by TeleAtlas (ESRI, 2004b). We also used a map of developed areas that was derived from a combination of NLCD land cover types, specifically urban classes, and Defense Mapping Satellite Program (DMSP) Operational Linescan System (OLS) imagery, which has the unique capability of detecting low levels of visible and near-infrared radiance at night. Elvidge et al. (2004) converted the year 2000 DMSP-OLS data to percent of impervious surface cover at 1 km resolution for the United States by augmenting the OLS imagery with a vector road database and urban cover classes derived from the circa-1992 NLCD map at 30 m resolution (Vogelmann et al., 2001). High resolution aerial photographs were used to provide calibration of a linear regression model in which the impervious cover estimates from photos were predicted from the combined OLS, land cover and roads data sets, resulting in 11.3% root mean square error in the linear model used to generate the map for observed values ranging between 0 and 90% (Elvidge et al., 2004).

We independently analyzed the accuracy of the OLS-NLCD impervious cover maps in earlier work and found them comparable to spatially aggregated higher resolution impervious cover maps generated directly from Landsat image reflectance data (Goetz & Jantz, 2006; Jantz et al., 2005). Nonetheless, we note again here that finer scale maps of proportional impervious cover have since been derived as part of the NLCD, but were not yet available for the analysis reported here and are still undergoing independent accuracy assessment. Finer-scale analyses may be possible with these data sets, following the same methodology we have developed for the current analysis.

Finally, we used a map of predicted future impervious cover developed for an area that includes the greater park ecosystem of the Upper Delaware River Park. This map was generated using a cellular automaton model calibrated to the rates and pattern of urbanization as mapped using Landsat imagery (Jantz & Goetz, 2007; Jantz et al., in press). We use here one future scenario of urban development (current trends/business as usual) predicted by the model to explore the potential loss of habitat connectivity as a result of continued residential development in this area. The scenario map was not used in the identification of core habitat areas, but simply as an overlay on the independently derived core area and connectivity map results (described below) to assess the vulnerability of specific locations to predicted land use change.

3. Methods

3.1. Core habitat

Core habitat was determined using a combination of road density, the amount of development (impervious cover) and tree cover within each grid cell. Our criteria were that core habitat should be no closer than 500 m to the nearest improved road and have a minimum size of at least 2000 ha (5000 acres). These values were selected to be consistent with current USDA Forest Service criteria for identification of remote roadless areas (USFS, 2001). After identifying core habitat areas, the mean impervious surface cover of each identified core area was calculated to remove human modified areas. The mean tree cover of each area was also calculated and those areas with values less than 60%, a commonly used threshold used to distinguish between “forest” (>60%) and “woodland” (30–60%) cover types (FAO, 2007), were removed from the initial analysis. We also assessed the impact of removing this criterion, as discussed below.

The density of roads within a 250 m grid was calculated such that each grid value reflected the linear distance of road per unit area (meters per square kilometer). A 250 m grain size was used to accurately capture the detail of core areas while constraining computational demands. Unimproved roads, generally defined as one lane dirt roads not passable by a standard passenger car, were excluded from the roads database, effectively permitting their presence in core areas. An exploration of alternative means of core area identification was conducted by Jantz and Goetz (2008), where the effect of unimproved roads and different buffer depths on core area identification was quantified. Contiguous groups of cells (i.e. core areas) meeting the minimum size threshold (2000 ha) were identified as discrete patches. Lakes, as identified using the 1:1,000,000 U.S. National Atlas (www.nationalatlas.gov/mld/hydrogm.html), occupied less than 4% of total identified core area and these were flagged as core areas not directly associated with terrestrial habitat.

Management status was identified for each core area, with the sole intent of identifying their ownership status for relevance to management objectives (i.e. GAP categories were not used in the process of identifying core areas, only in assessing their ownership). We note here that, at the landscape scale, a diversity of management practices may be expected to produce a greater diversity of habitats which, in turn, would be expected to support greater biodiversity (e.g. Gustafson et al., 2007). Because any given core area may fall under more than one management regime, metrics were calculated on portions of the core areas within the specific GAP ownership categories. GAP categories 1 and 2 were grouped because of their similar status of protected lands, including parks, and their emphasis on preserving landscapes and protecting biodiversity. While the data set did not include comprehensive data for private lands in the study region, we assumed that stewardship information for governmental entities was complete and any area not owned by federal, state, county, or local governments was private and unprotected and would therefore not be classified as a protected area. Analyses for locales where these data are available would permit their consideration in comparable analyses to those we describe here.

Finally, fragmentation metrics were calculated using Fragstats 2.0 (McGarigal et al., 2002), including the number, mean area, and mean perimeter to area ratio of all core areas within the same management status. We also specifically compared metrics for core areas under the jurisdiction of three Federal agencies responsible for natural resource protection and management: the United States Fish and Wildlife Service, the National Park Service, and the United States Forest Service.

3.2. Connectivity

Connectivity between core areas was calculated using a graph theoretic approach. Graph theory provides a useful framework for assessing potential ecological connectivity because it allows inclusion of continuous variables that are relevant surrogates of landscape traversability (permeability) such as road density and forest cover (Bunn et al., 2000; Urban, 2005; Urban & Keitt, 2001). The availability of detailed remotely sensed and other spatial data sets makes the approach particularly useful for assessing connectivity over large areas. Core area connectivity was approached from the perspective of a theoretical, terrestrial, forest dependent species with no dispersal threshold and no defined time period for dispersal. Our assumption was that higher forest cover areas would be more traversable for the theoretical species and that human disturbance (roads, development, and agriculture) and water barriers would decrease traversability by terrestrial organisms. We recognize that this is a simplified assumption and that the motility and dispersal of different organisms will be differentially influenced by the amount of forest cover, e.g. wolves and weasel family predators would be more sensitive to forest cover than deer or grazing ungulates. We also recognize that this assumption is more relevant to the temperate forests of the eastern United States

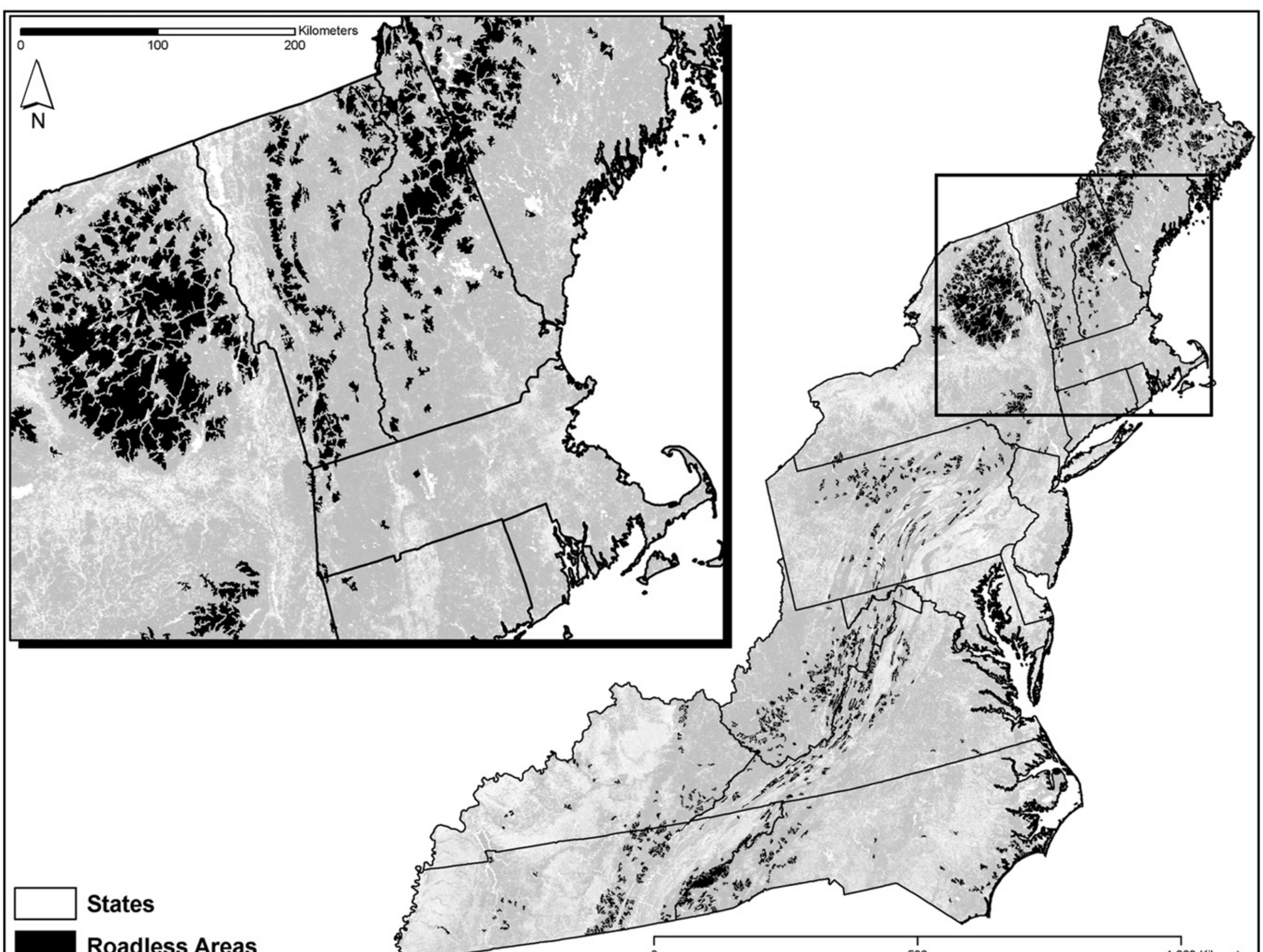

Fig. 1. Roadless core habitat areas in the eastern United States identified using the approach described in Section 2. The background (shades of gray) is the 1 km resolution MODIS tree cover product. The inset image shows detail for an area centered on Vermont and New Hampshire.

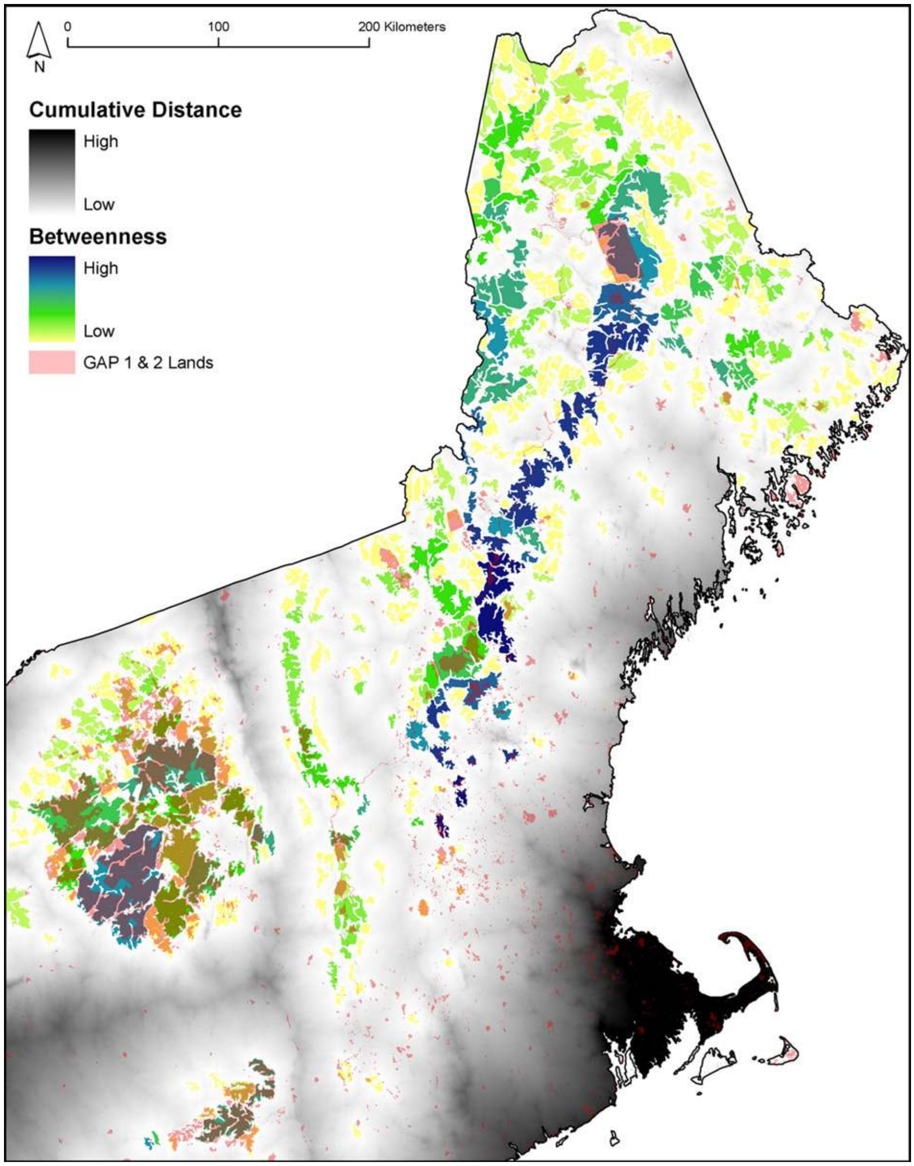

Fig. 2. The 'betweenness' connectivity metric for the northeastern portion of the study region. A cumulative cost surface (described in Section 3) is shown in the background (grayscale). Betweenness values range from yellows (low) to blues (high). The high values running through the center of the region indicate a high density of least cost paths traversing those core habitat areas.

than to more open forest habitat mosaics of, e.g., mountain ecosystems of the western U.S.

A suitability or cost surface incorporating tree cover, impervious surface cover, road density, and water bodies was created to calculate the functional distance between core areas. Cells with lower tree cover values were thus more costly to traverse, and cells with higher values of tree cover the inverse. The road density data were scaled to a range 0 to 100, to match the range of values in the impervious and tree cover maps, with higher values being more costly to traverse. Each data layer (road density, impervious cover and tree cover) was considered to have equal weight in the development of the cost surface, resulting in a final suitability surface map with values between 1 and 300. Water bodies, as noted above, were essentially omitted by assigning the highest cost (lowest suitability) value of 300.

Connectivity was assessed with recently developed software called ArcRstats (www.nicholas.duke.edu/geospatial), which uses a graph theoretic approach to identify the least cost paths between core habitat areas from which network centrality metrics are calculated. ArcRstats (version 0.7, released 2006-06-27) required two inputs, habitat patches (i.e. core areas) and a cumulative distance surface, derived from the cost surface, the values of which indicate the distance from a particular cell to the nearest habitat patch, taking the cost of traversing intervening cells into account. Connectivity metrics were derived from least cost paths between core areas, allowing for evaluation of each area's contribution to different aspects of overall landscape connectivity. The cumulative distance grid was converted to a triangulated irregular network (TIN), which is a three dimensional surface

Table 1

Statistics on core habitat area under each management category, where categories 1 and 2 are parks and other protected areas, and other categories are as described in Section 2.1.

Management	Area (km^2) and proportion (%)	Number and proportion (%)	Mean area	Median area	Perimeter/ Area ratio
Category 1 or 2	17,178 (23)	1180 (12)	15	0.9	75
Category 3	30,831 (42)	1786 (18)	17	1.4	68
Category 4	25,360 (35)	6796 (70)	4	0.2	100

Proportions sum to 100%.

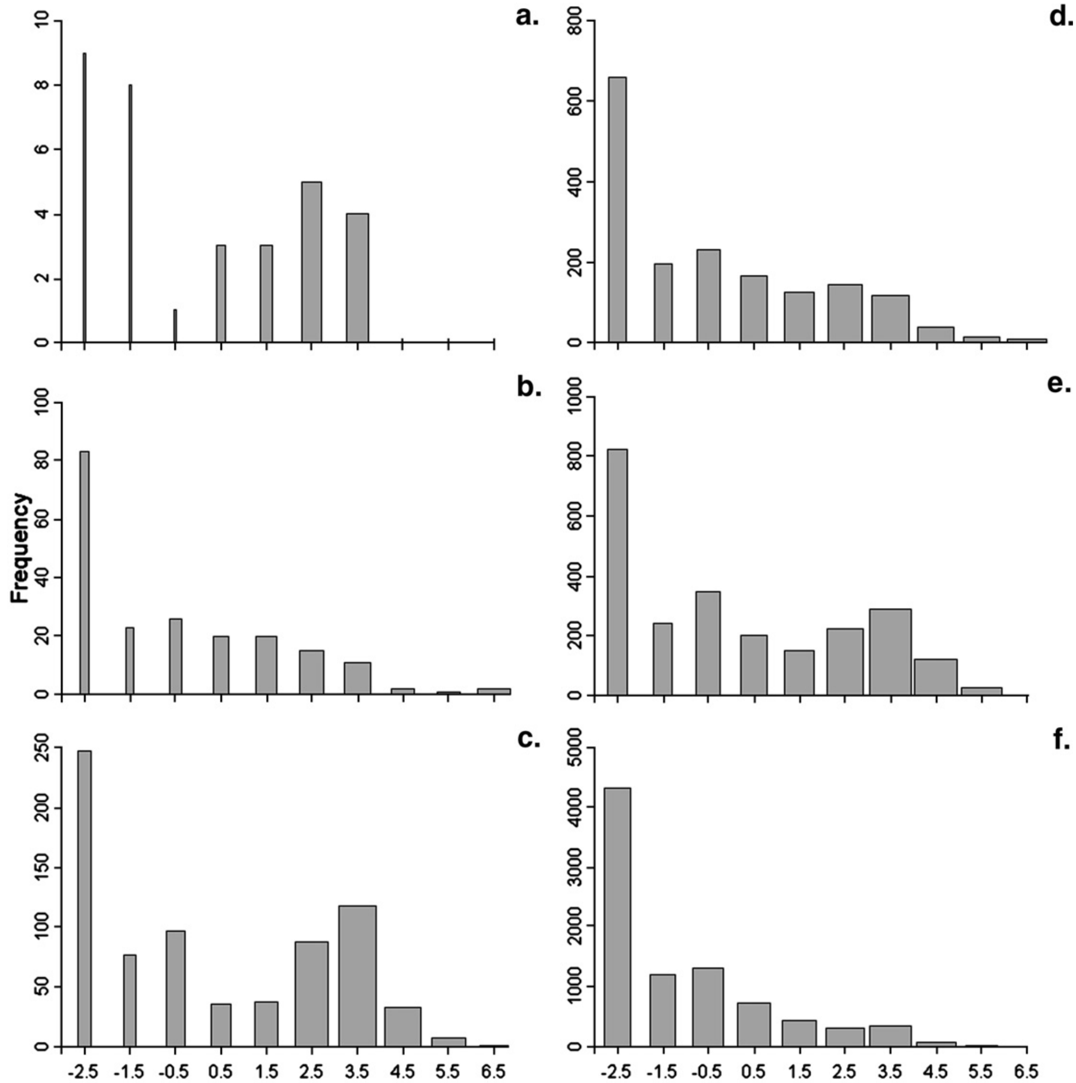

Fig. 3. Patch size frequency for core areas managed by (a) U.S. Fish and Wildlife Service, (b) U.S. National Park Service, (c) U.S. National Forest Service, (d) GAP 1 and 2 management, (e) GAP 3 management, (f) GAP 4 management. Bar width corresponds to the log of the total area of patches within each bin. Note that the *Y*-axis (frequency) varies. GAP categories 1 and 2 are parks and other protected areas, and other categories are as described in Section 2.1.

representation. Additional details of the process are described by Urban and Keitt (2001) and Jantz and Goetz (2008).

The fraction of least cost paths that pass through each core area (betweenness) and the relative distance to all nodes from each core area (closeness) were calculated as landscape metrics, and the fraction of possible nodes connected to each core area (degree) was calculated as a patch level metric. Each metric has similar directionality with respect to conservation value, thus core habitat areas with high betweenness, closeness and degree values provide the best landscape connectivity. We summarized these metrics by management status and assessed their significance for connectivity across the region.

4. Results

4.1. Core habitat

Large numbers of core areas were identified in northern and western Maine, and these extended south into New Hampshire where large core areas were contained within the White Mountain National Forest (Fig. 1). A linear strip of core areas also extended along the north–south axis of Vermont within the Green Mountain National Forest. Significant core areas were also contained within the Great Smoky Mountains National Park in Tennessee (discussed further below). The Adirondack and Catskill State Parks in New York contained relatively isolated but large clusters of core areas, including the single largest (1932 km^2), as did mountainous areas of the ridge and valley physiographic province. The remaining areas were sparsely distributed across the study area, mostly along the ridges of the Appalachian Mountains. A total of 1177 discrete core areas covering 73,370 km^2 were identified, comprising approximately 8% of the study region.

Table 2
Statistics on core habitat area by major public agency ownership across the study region.

Public agency	Area (km^2) and proportion (%)	Mean area	Median area	Mean perimeter/ Area ratio	Median perimeter/ Area ratio
National Park Service	2410 (19)	19.3	1.2	80	75
Fish & Wildlife Service	204 (2)	7.3	1.7	70	50
National Forest Service	10,032 (79)	18.8	3.6	62	39

National Park Service and Fish and Wildlife Service lands fall under GAP categories 1 and 2 (most protected), whereas National Forest Service lands fall under category 3 (less protected). Proportions sum to 100%.

Removing the 60% tree cover threshold criteria increased the total amount of core area identified by just 5% (3333 km^2), with the greatest total increases in North Carolina and Maine.

4.2. Connectivity

Core area betweenness values varied across the study area, but a major corridor was apparent running north/south through New England and the Ridge & Valley physiographic province (Fig. 2), indicating high levels of landscape permeability in the region. Core areas in the central part of the study area had higher values of the closeness metric, indicating greater clumping of core areas than to either the north or south. Larger, centrally located core areas also had higher values of the degree metric than peripherally located areas, indicating greater node connectivity.

Of Federal lands, those under the management of the National Park Service had degree values twice as high as Forest Service or Fish & Wildlife lands, indicating Park Service holdings were better connected than other federally managed lands. The Park and Forest Service lands also had high betweenness values, whereas Fish & Wildlife lands had both low betweenness and degree values. Closeness values were similar across all federal lands.

4.3. Protected areas

Roughly 20% of the core area we identified (17,178 km^2) is currently protected from development and has strong land use controls, i.e. GAP category 1 or 2 lands (Table 1). Conversely, almost 80% of core areas are subject either to development or management activities that could modify habitat quality. Removing the tree cover threshold of 60%

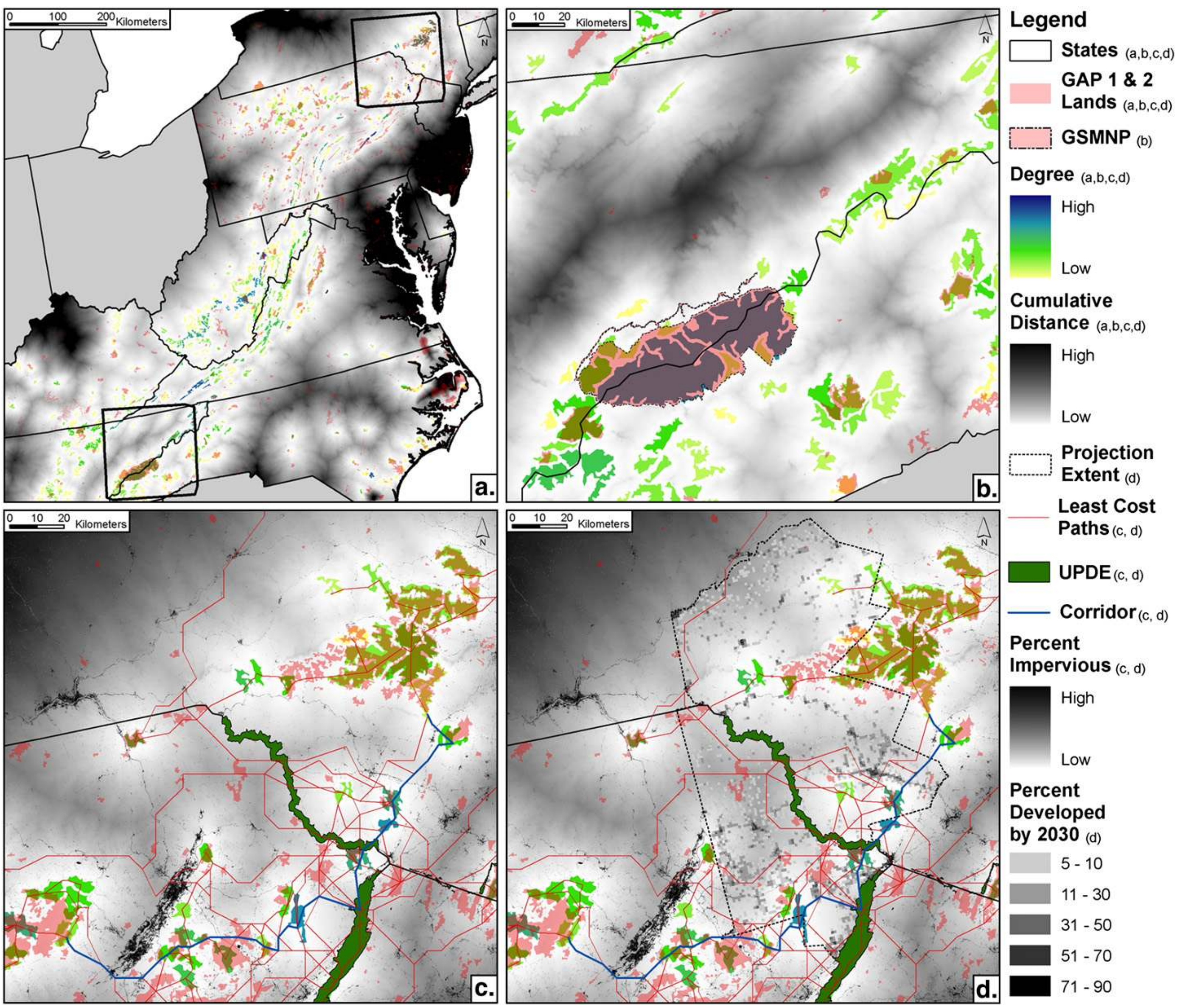

Fig. 4. Analysis of connectivity in the study region with boxes outlining those areas analyzed in the other panels (a), including the Great Smoky Mountains National Park (b) and the Upper Delaware Scenic River and Delaware Water Gap National Parks shown in green (c, d). The 'degree' connectivity metric is shown, with values ranging from yellows (low) to blues (high). Major least cost paths between core habitat areas are overlaid as red lines, showing primary connectivity routes derived using the graph theory approach. In panels c and d urban and residential development from the NLCD impervious cover products (as described in text) are shown in black, and one of the primary least cost paths connecting core habitat areas is highlighted (in blue). Urban development predicted to occur by the year 2030 is shown in panel d for the four counties encompassing the parks (indicated by a dashed line). The predicted expansion of impervious cover has a spatial resolution of 1 km, compared to the 30 m NLCD impervious cover depicted outside the four county area. In the legend, letters in parentheses indicate the panel(s) in which a layer is depicted.

increased the amount of core area identified in categories 1 and 2 lands by just 3%. Statistics of parks and protected areas are also compared to other GAP category lands in Fig. 3. Mean core area was lowest for the least protected lands (category 4) and about comparable for the other ownership categories. The median size of core areas was greatest in category 3 ownership, which is dominated by state and national Forest Service lands. Perimeter to area ratio was highest for category 4 lands, reflecting their smaller patch sizes and greater amount of edge habitat. Perimeter to area ratios were better and more comparable in the other ownership categories.

Federal lands made up 12,646 km^2 of the study area (Table 2). Forest Service lands made up the majority (74%) of this, and an even higher proportion of the total amount of identified core habitat (79%) (Fig. 3). National Park Service and Fish & Wildlife Service lands comprise smaller proportions of the study region and the lands identified as core habitat (19% and 2%, respectively). Fish & Wildlife Service lands occupy 10% of Federal lands in the region but very little of the identified core area, reflecting the small patch sizes of these holdings. Forest Service lands had a mean core area close to that of Park Service lands but a median core area three times as high, indicating many larger core areas under Forest Service jurisdiction. Mean and median perimeter-to-area ratios were highest for Park Service lands and lowest for Forest Service lands, reflecting the smaller size and narrow linear shape of many of the parks along rivers and ridgelines (e.g. the Blue Ridge Parkway).

Local examples of protected areas in a landscape context are shown for the Great Smoky Mountains National Park (GSMNP) on the border of North Carolina and Tennessee, and the Upper Delaware National Scenic River (UPDE) on the border of Pennsylvania and New York (Fig. 4). In the case of GSMNP, which is a world heritage site, one of the most visited units in the National Park system, and contains threatened and endangered species, the park encompasses what we have identified as two large but disjunct core habitat areas, bisected by a primary road (route 441 between Gatlinburg TN and Cherokee NC). Areas to the north and west of the park are dominated by development (including Knoxville TN), which is reflected in the cost surface depicted in Fig. 4 (panel a). Core areas that connect the park to additional habitat are concentrated along the spine of the southern Appalachian mountain chain, extending in a narrow strip to the northeast and southwest, and to areas in the Nantahala National Forest to the southeast (panel b).

The influence of development isolating habitat is even more evident around the UPDE Park (Fig. 4, panels c and d). In this case, we have overlaid impervious surface cover from the NLCD as well as our projections of future development expected by the year 2030 (Jantz & Goetz, 2007; Jantz et al., in press). The park, which is elongated and narrow and thus not well reflected in our core habitat area maps, is surrounded by fragmented forest habitat undergoing rapid exurbanization on the rural–urban fringe (Fig. 4, panel c). A portion of the greater New York City metropolitan area is visible to the southeast, and the town of Scranton Pennsylvania to the west. One of the four counties that surround the park (Pike) was the fastest growing county in the nation in 2006. There is little core habitat adjacent to or in close proximity to the park, but our connectivity metrics (Degree is shown in Fig. 4) identifies a set of corridors that could link UPDE with the Catskills state park to the northeast, and a set of core areas in central Pennsylvania, including the World's End state park, which could form a more functional greater park ecosystem. Note, however, the amount of predicted development (Fig. 4, panel d) in areas where least cost paths linking core habitat were identified, indicating the likely loss of connectivity in the near future under a business as usual development scenario. Because this development is predicted to intensify over the coming decades, as shown in our spatial modeling of future urbanization, local jurisdictions are working with the Park Service to ensure future viability of the ecosystem, as well as the local economies that are depend upon recreation and tourism.

5. Discussion

Wildlife habitat on private lands increases the effective size of the nation's reserve network and thereby enhances both ecosystem integrity and the conservation of biodiversity (DeVelice & Martin, 2001; Loucks et al., 2003; Noss et al., 1999; Strittholt & Dellasala, 2001). The public versus private ownership of core habitat areas that we have identified varies considerably, but over a third of the areas are in management regimes that offer no specified legal protection. Another 42% are protected from development but subject to activities that can modify the quality of biological resources (e.g. motorized use and commercial logging). Thus, close to 80% of the core areas identified are subject to uses which may decrease their contribution to the functionality of ecosystems or the conservation of biodiversity. The degree of protection varies considerably from state to state. In general, the largest core areas we identified were associated with national or state parks and forests. An exception to this observation were the large industrial forests of Maine, which have undergone recent changes in ownership (over 11,000 km^2 in the period 1994 to 2005) that resulted in much less land use focused solely on commercial timber production (Hagan et al., 2005).

We note that private lands were not systematically surveyed for development of the protected areas database (Loucks et al., 2003), likely leading to an underestimate of the extent of core area on private lands that falls under some sort of protected status, although fee-simple holdings of conservancies were included. National conservation organizations and numerous regional, state, and local land trusts are placing lands under conservation easements across the Eastern U.S. (Aldrich & Wyerman, 2006). For example, the Pingree easement, one of the largest conservation acquisitions in history, covers a group of parcels arrayed primarily across northern Maine totaling roughly 762,000 acres (3084 km^2). This parcel, which is managed for multiple forms of public recreation as well as timber extraction, is not explicitly reflected in the version of the protected areas database used in our analyses. However, as most land areas in northern Maine are already classified as category 3, the impact on our management analysis is likely smaller than the total easement area implies. States in the study area experiencing substantial (>40,000 ha) increases in protected lands from 2000–2005 include Maine, Pennsylvania, Virginia, and Vermont, and these are where we expect underestimation of private protected core areas (Aldrich & Wyerman, 2006).

Relatively few of the identified core areas were open vegetation types, such as marshes where tree cover is perennially low, thus removing the 60% tree cover threshold as a criterion had a small effect the total area identified as core area (increasing it by 5%). Setting a tree cover threshold was probably most useful for eliminating other land uses (e.g. agriculture) from consideration. This result indicates that most of the core areas in the east already have high densities of tree cover, although the condition of these forested areas likely varies based on allowable land uses. On categories 3 and 4 lands in particular, one might expect to find evidence of recent anthropogenic disturbance which, depending on the scale and type of disturbance (e.g. clear-cut logging versus selective harvesting), will have different impacts on a range of species.

In related work we show that the extent of core area identified is sensitive to assumptions made about different road types and how far their influence extends from the road edge (Jantz & Goetz, 2008). For example, using an 800 m buffer depth (rather than 500 m) and allowing no unimproved roads reduced the extent of core habitat area by about half (to 36,802 km^2) in this study region. Nonetheless, compared to the current reserve network, there is a considerable amount of unprotected roadless core habitat remaining in the eastern United States, mostly falling under National Forest Service ownership.

There were differences in the patch and fragmentations statistics between management categories, where unprotected Category 4 lands generally consisted of a large number of small patches, with high perimeter to area ratios. The latter indicates patches with more edge, making them less insulated from exotic, invasive and parasitic species (Robinson et al., 1992). Category 3 lands comprised larger core areas with lower perimeter to area ratios than those in a more protected status. Among Federal lands, the relatively low proportion of Fish & Wildlife Service core areas is likely a result of the tendency for these lands to be located in small but locally important wetlands complexes. Fragmentation indices for federally managed core areas indicate that Forest Service lands compare favorably to Park Service lands, especially when considering median core area size and perimeter to area ratios. The relatively poor perimeter to area ratios for Park Service lands are likely driven by linear Park Service units along river networks and the Appalachian Trail (see Fig. 4).

The connectivity metrics provide a unique perspective on the potential habitat in the region, with information content that is more useful for management action or acquisition targeting than statistics on the extent, length or shape of specific corridors (see Calabrese & Fagan, 2004; O'Neill et al., 1997; Urban & Keitt, 2001). Recall that betweenness is a landscape metric that represents the fraction of least cost paths that pass through each core area, whereas closeness is a landscape metric that captures the distance to all nodes from each core area. In our analysis, betweenness values were highest for a linear set of core areas in New England, indicating high conduciveness to dispersal within the region. Closeness values were highest in the central part of the study region, producing a pattern similar to what one would expect when measuring average distance between all core areas. The degree metric, in contrast, is a patch level metric that depicts the fraction of possible nodes connected to each core area. Degree values were highest for large, centrally located patches, reflecting their connectivity with a large proportion of other core habitat areas. Some unprotected core areas in the study area had both high betweenness and degree values, indicating their importance for both local and regional connectivity. High value corridors that we have identified on private lands would be particularly suitable to efforts establishing conservation easements in a broader landscape context.

The high degree values for Park Service lands resulted from a combination of relatively large core areas and the adjacency of Forest Service lands, which act as buffer areas in the surrounding landscape. The relatively small extent of Fish & Wildlife Service units contributed to low connectivity for these lands, which is again consistent with these holdings representing primarily unique and rare habitats in the eastern U.S., rather than large areas of diverse habitat. Finally, we note that betweenness values for many private (category 4) core areas were as high or higher than adjacent core areas on public lands, indicating their potential for contributing to much needed landscape connectivity in the region.

Our analyses of specific Park Service units (Great Smoky Mountains and the Upper Delaware Scenic River) support the findings of the more regional analysis, and identify local core area holdings that can be connected to expand the effective greater park ecosystems. Using this type of analysis, together with other habitat conservation strategies including the emerging state wildlife action plans, would help ensure that parks and protected areas are sufficiently connected and protected from rural residential development. The tools and data sets used here are widely available and can help resource managers to identify priority habitat for improving ecosystem integrity and better plan for future development in the landscapes surrounding protected areas.

6. Conclusion

Development pressures that threaten core habitat and connectivity are intensifying across much of the nation in the form of low density residential development. Increased conversion and fragmentation of unprotected core habitat by this exurban development will complicate efforts to preserve intact functional ecosystems in existing parks and protected areas. If current trends continue, increased fragmentation and conversion by development of many of the core areas we identified in the Eastern temperate forests is likely, particularly because nearly 80% remain unprotected. Not only would this be an important loss of habitat area, but would further isolate habitat islands, decreasing successful dispersal and increasing the likelihood of local species extinctions, particularly in the context of changing climate.

The data on forest cover and the built environment used for this analysis, both derived from satellite remote sensing, allowed for ecologically meaningful analyses of core habitat areas and their connectivity within the context of parks and protected area management. Because the tools we used are widely available to users and some even finer resolution data sets are now available in a consistent form nationwide, similar analyses could be conducted to assess the extent and status of core areas across any other region for natural and protected area management and planning objectives. The development of comparable or improved data sets at the global scale (e.g. Elvidge et al., 2007; Hansen et al., 2003) means that similar analyses can also inform practical protected area management around the world, subject to regional validation and verification efforts.

We believe our findings have relevance to issues of how current protected areas function in the context of surrounding lands that may be subject to different human use or management objectives, and that the results are not unique to the geographic region we analyzed. Our results suggest a starting point for the construction of a more comprehensive reserve network for the study region, and a means to consider protected areas in a landscape context. Additional studies of similar scope would help to inform this subject and possibly lead to improved methods to conduct conservation in a broader landscape context, including incentives for private land owners to enhance the management objectives of protected areas. Acquiring or negotiating development rights for remote areas on private lands, and increasing the number of designated wilderness areas on public lands for incorporation into a larger reserve network, would facilitate the preservation of remaining core habitat and associated biological diversity and ecosystem integrity.

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