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ABSTRACT

Following federal protection in 1974, gray wolves (*Canis lupus*) partially recolonized former range in the western Great Lakes region, USA, yet remain absent from most of the eastern USA. Understanding potential for further recolonization requires quantifying remaining wolf habitat and habitat connectivity. We used recent snow tracking data from the western Great Lakes region to create an ensemble distribution model to estimate areas of habitat large enough to support gray wolf populations in the eastern USA. We then modeled cost-weighted distances between these areas and circuit connectivity to identify potential linkages. Our final distribution model had good performance (Receiver Operator Characteristic = 0.87) and suggests wolves selected against areas with greater human population densities and proportions of agricultural land. Gray wolves currently occupy about 4 % of their historical range in the eastern USA, which represents 12 % of the area estimated to remain suitable. We estimated 35 % of former range is currently suitable for wolves, and 18 % of these suitable areas are protected, mostly under state and federal jurisdictions. We identified five unoccupied areas where wolves could establish viable populations ranging from 18,110 to 725,488 km^2. Connectivity between these areas and current wolf range is limited primarily by the Great Lakes and extensive agriculture in the Midwest USA. Most core habitat areas and priority linkages cross state or country borders, highlighting the importance of interjurisdictional cooperation. Our estimates of remaining suitable range and the potential for recolonization provide a baseline for the development of policies on gray wolf conservation in the eastern USA.

1. Introduction

Worldwide, geographic ranges of large carnivores have contracted markedly since the 1700s due to anthropogenic causes (Ripple et al., 2014; Wolf and Ripple, 2017), primarily persecution (Musiani and Paquet, 2004) and habitat and connectivity loss (Crooks et al., 2011), which are linked to increases in human populations and land use change (Woodroffe, 2000). Range contractions of over 20 % have occurred for 80 % of large carnivore species, particularly in regions with high livestock densities (Wolf and Ripple, 2017). Human encroachment on large carnivore habitat also increases potential for conflict with humans (Boudreau et al., 2022), which can result in direct carnivore mortality and reduce public support for their conservation (Treves and Karanth, 2003; Treves and Bruskotter, 2014).

A better understanding of ecological top-down effects has increased recognition of the importance of large carnivores (Ripple et al., 2014). Together with improvements in public perceptions (Chapron et al., 2014; Gompper et al., 2015), policymaking has shifted and coexistence has become a more prevalent management objective (Linnell et al., 2001). Improved coexistence with large carnivores has contributed to partial reoccupation of former range in the United States (Gompper et al., 2015) and Europe (Chapron et al., 2014), though range contractions continue for many species, particularly in Africa and Asia (Wolf and Ripple, 2017). Recolonization of former range by large carnivores depends in part on habitat connectivity (Hemmingmoore et al., 2020). However, connectivity can be reduced by habitat fragmentation (Crooks et al., 2017), to which these species are especially vulnerable due to their low densities and large territories (Crooks et al., 2011).

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Maintaining viable populations of large carnivores requires large areas, often thousands of square kilometers (USFWS, 1992; Wielgus, 2002), yet only 5.2 % of their habitat worldwide is estimated to have protected status (Crooks et al., 2011), requiring dispersal through, or persistence in, non-protected landscapes with high human disturbance (Boron et al., 2016). This suggests that land sparing, by protecting areas relatively free from human disturbance, but also land sharing, by tolerating large carnivores in unprotected areas, are critical for recolonization of former range by large carnivores (Chapron et al., 2014; Gompper et al., 2015).

In Europe and North America, species such as gray wolf (*Canis lupus*), Eurasian lynx (*Lynx lynx*), and American black bear (*Ursus americanus*) have recolonized former range following increased legal protection of large carnivores and their habitat (Linnell et al., 2001; Smith et al., 2016). Since 1974 gray wolves have received federal protection in the contiguous USA through the Endangered Species Act (ESA) (Ruid et al., 2009), with periods wherein protection was removed for some populations (Bergstrom et al., 2009; Olson et al., 2015). Currently, the largest wolf population in the contiguous USA is the western Great Lakes distinct population segment, which occurs in portions of Minnesota, Wisconsin, and Michigan, and contained around 4200 gray wolves in 2020 (USFWS, 2020a). Wolf habitat in other eastern USA states has been identified in New York, Vermont, New Hampshire, and Maine (Mladenoff and Sickley, 1998), and 15 states in the Midwest region (Smith et al., 2016), but there are no assessments of remaining habitat throughout former range across the eastern USA (Nowak, 1995; USFWS, 2009). Gray wolf populations are estimated to require 25,600 km^2 or 12,800 km^2 for viable independent or immigration-dependent populations, respectively (USFWS, 1992). However, there has been no assessment of where natural recolonization of former range is plausible, considering habitat availability and landscape connectivity.

Most gray wolf mortality in the USA is human-caused (Hill et al., 2022), and recolonization of former range in the eastern USA may depend largely on human tolerance, highlighting the need for conflict prevention and mitigation (Treves et al., 2004). Estimating habitat for gray wolf establishment and identifying linkages that might facilitate movement could assist development of management strategies and policy. Assessing the role of protected and non-protected areas in wolf recolonization is particularly important to management and policy planning, as human-wildlife conflicts are more likely in non-protected areas with greater human disturbance (Treves and Karanth, 2003, but see Reinhardt et al., 2019). Additionally, evaluating natural recolonization potential can help identify areas where re-establishment within former range is unlikely without human assistance, or where former range has become unsuitable.

We developed a distribution model to estimate current wolf range in the western Great Lakes region and used it to predict habitat availability throughout former wolf range in the eastern USA, expecting wolf habitat to occur mostly in areas with low human disturbance and greater proportions of natural land cover. We also estimated habitat connectivity, including southern Canada, to identify potential linkages that could connect unoccupied areas with currently occupied areas. Finally, we evaluated the ownership status of protected suitable areas, potential linkages, and identified areas likely suitable to maintain viable wolf populations.

2. Methods

2.1. Study area

Our study included the former range of wolves in the eastern USA (Nowak, 1995), and adjacent southern Canada of which most is currently occupied by wolves (Wolf and Ripple, 2017). We used the Area of the Undertaking of Ontario (Hunt et al., 2005), the zone where forests are managed by the province, as the northern limit of the study area (Fig. 1). The overall area excluding water is 4,187,681 km^2, of which about 60 % is natural land cover (e.g. forests, grasslands, shrubland), 33 % is agricultural land, and 7 % developed (Homer et al., 2017). Elevations are 1–2436 m above sea level (USGS, 1996), with higher elevations in the western part of the study area and the Appalachian range in the east.

2.2. Data collection and processing

We used winter wolf track survey data collected by the Departments of Natural Resources (DNR) of Minnesota (2018), Wisconsin (2018–2020), and Michigan (2018, 2020). In Minnesota, trained natural resource professionals were instructed to record locations of all wolf sightings and signs (e.g. tracks, scat) observed from November until snowmelt, usually mid-April (Erb and Sampson, 2013). Participants could record locations on forms or maps, but most used a web-based GIS application. The final dataset was combined with presence data recorded during other surveys coordinated by the DNR (e.g. furbearer survey, carnivore scent station survey). In Wisconsin, DNR staff, tribal biologists, and trained volunteers conducted surveys throughout known wolf range, primarily during December–April (Stauffer et al., 2020). The survey area included 164 survey blocks of approximately 500 km^2 each, delineated using waterways, roads, and state boundaries, ensuring each block could be surveyed within a day. Surveyors attempted to survey most snow-covered roads within a block 1–3 days after snowfall and blocks were surveyed on average 2.8 times. In Michigan, the Upper Peninsula is divided into 21 survey blocks from which a stratified random sample of 12–13 survey blocks are selected for surveys every other year, representing ≥60 % of the total area (Michigan Department of Natural Resources, 2008). Michigan Department of Natural Resources staff were assisted by US Department of Agriculture Wildlife Services personnel, and surveys occurred during December–April. Searches for wolf tracks and other sign occurred along trails and roads by truck or snowmobile. Only the Upper Peninsula was surveyed as wolves are not established in the Lower Peninsula of Michigan (Michigan Department of Natural Resources, 2008).

We filtered snow tracking data to one presence point per 1 km^2 across all years to reduce spatial autocorrelation (Gantchoff et al., 2021), resulting in 3689 presence points. Within the entirety of each state, we randomly generated twice as many pseudo-absence points as there were presence points (Barbet-Massin et al., 2012; Appendix A). Assigning pseudo-absences throughout former range would imply a mismatch between the environment currently unoccupied and the ecological niche of wolves, yet wolf absence in most former range is thought to be primarily a consequence of historic anthropogenic activities (Wolf and Ripple, 2017) rather than a consequence of differences in physical landscape features (Nowak, 1995). We then removed duplicate points, pseudo-absence points located in water, and pseudo-absence points on Isle Royale National Park, Michigan (USA), where wolves are present but we did not have survey data.

2.3. Ensemble modeling

We used six variables to model wolf presence in the western Great Lakes region. We used the North American Land Change Monitoring System (30-m resolution; Homer et al., 2017) to derive proportions of, and distances to, agricultural land (class cropland), and natural land (all other classes except water and ice and snow) (Fig. 1). We excluded areas of the land cover class water from the model, as water bodies are typically not considered wolf habitat. We combined all natural land covers into a single class, because vegetation types in current wolf range, where presence points for the model originate, differ from parts of former wolf range. This mismatch could result in former range being estimated unsuitable based on vegetation differences, despite wolves being adaptable to most ecoregions ((Nowak, 1995). For human popu-

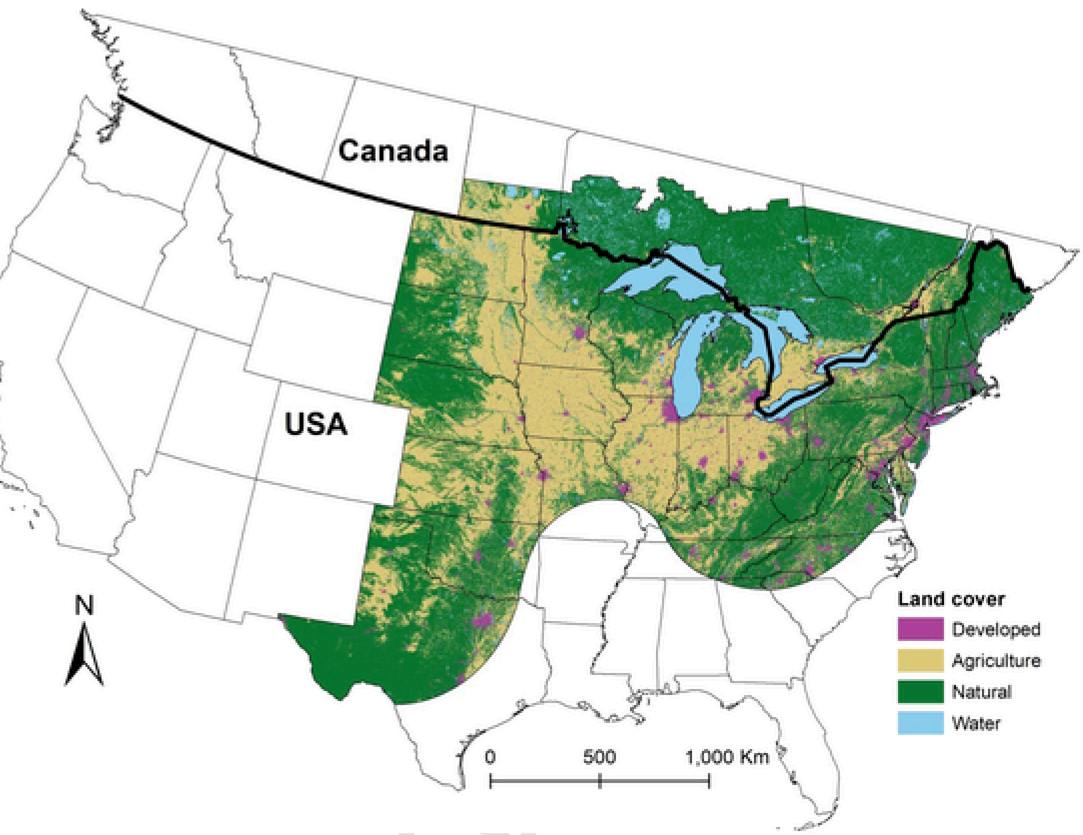

Fig. 1. Land cover throughout former range of gray wolves (*Canis lupus*) in the eastern USA (Nowak, 1995) and southern Canada approximating the northern limit of forest management in Ontario.

lation density we used the Gridded Population of the World (v4.11) database (30-arc-seconds resolution; CIESIN, 2020). We used the USGS GTOPO30 digital elevation model for elevation (30-arc-seconds resolution; USGS, 1996). Before calculating proportional land cover variables, we rescaled variables to 1-km resolution to reduce spatial mismatch between species data and environmental data (Guisan and Thuiller, 2005). Because wolf surveys were mostly conducted along roads, leading to positive bias between wolf presence and variables related to developed land cover and road density, we did not include distance to, and proportion of, developed land cover, or road density (Gantchoff et al., 2022). As road density has been found negatively related to wolf habitat selection in distribution models (Jędrzejewski et al., 2008; Mladenoff et al., 2009), we used alternative variables relating to human populations and agricultural activities as proxies for human landscape disturbance (Smith et al., 2016). We used variance inflation factors (VIF) and pairwise correlations to test for multicollinearity of variables. For variables with pairwise correlation >0.70, we created test models with only one of the correlated variables, and removed the variable which resulted in lower fit from the final model. This was done until all pairwise correlations were <0.70 and VIF scores were <10 (Guisan et al., 2017).

To reduce potential for overprediction of wolf habitat using single models (Marmion et al., 2009), we developed an ensemble model with 10 submodels (Thuiller et al., 2009): artificial neural network (ANN), random forest (RF), mixture discriminant analysis (MDA), maximum entropy (MaxEnt), generalized linear model (GLM), generalized additive model (GAM), generalized boosted model (GBM), multivariate adaptive regression splines (MARS), surface range envelope (SRE), and classification tree analysis (CTA). We created the ensemble model and extrapolation beyond current range using the biomod2 package (Thuiller et al., 2009) in program R 3.6.2 (R Core Team, 2020). We used 70 % of data to calibrate the model and the remaining 30 % to evaluate model performance, repeating this procedure three times (Guisan et al., 2017). We used the area under the curve (AUC) of the receiver-operating characteristic (ROC) and the True Skill Statistic (TSS), and their associated sensitivity and specificity scores, as evaluation metrics (Allouche et al., 2006). We considered AUC scores >0.90 as "excellent", $0.90 > x > 0.80$ as "good" and $0.80 > x > 0.70$ as "fair" (Araújo et al., 2005) and limited the ensemble model to submodels with a TSS score ≥ 0.5 (Gantchoff et al., 2021). We assigned weights to submodels that were retained, proportional to their respective evaluation scores, and averaged them using an ensemble model for the western Great Lakes region, and a projection to former wolf range in the eastern US. We assessed variable importance by calculating correlations between fitted values and three randomly permutated values of each variable (Thuiller et al., 2009). As resulting values are automatically inverted, low correlation numbers imply low contribution of each variable to the model. We used response curves of the variables with greatest importance to assess their effects on likelihood of wolf presence (Elith et al., 2005).

2.4. Estimating connectivity

We first classified core areas of habitat by transforming the landscape suitability map to a binary format, using an optimized probability threshold resulting in maximized TSS scores in Biomod2 (Thuiller et al., 2009). We defined core areas as habitat patches $\geq$100 km^2, representing the smallest plausible annual home range (Stauffer et al., 2020). Patches separated $\leq$2 km were merged (Gantchoff et al., 2020), considered reasonable as wolves can travel up to 72 km in 24 h (Mech and Boitani, 2003). Because wolves might use lower-quality habitat than residents (Keeley et al., 2016), we created a resistance surface raster using a c8 exponential transformation (Zeller et al., 2018) rather than assuming an inverse relationship between habitat suitability and landscape resistance. Though wolves cross frozen lakes and rivers during winter (Orning et al., 2020), these conditions occur only several months each year in northern portions of our study area. We therefore assigned maximum resistance scores to 1-km cells classified as water to better represent overall natural barriers to dispersal, as the maximum distance recorded for swimming wolves is about 2 km (Darimont and Paquet, 2002).

To map linkages, we calculated least-cost paths (LCP) between core areas using the LinkageMapper toolbox in ArcGIS (McRae and Kavanagh, 2011), and created linkages by buffering 1 km on either side of LCPs. We calculated cost-weighted distances (CWD) of linkages by summing resistance values we derived from the resistance surface raster, using cells that intersected with linkages (Zeller et al., 2018; Gantchoff et al., 2021). Linkages between core areas are categorized as having low, medium or high connectivity using equal intervals of their total CWD, whereby a lower CWD implies higher landscape connectivity. We used the Linkage Priority tool to assign linkage importance, equally weighted using linkage permeability, and the proximity and value of core areas connected by this linkage (Gallo and Greene, 2018). We calculated core area values based on area size, centrality, landscape resistance, and area/perimeter ratio. To further assess landscape-level connectivity without the assumption of animal landscape knowledge, we used Circuitscape software (McRae and Shah, 2020). We assigned 310 points at 40-km intervals around the perimeter of the study area and calculated connectivity between all pairs of points, providing an omnidirectional connectivity map for animals moving randomly through the landscape (Gantchoff et al., 2021).

2.5. *Core area protection status and size*

We assessed the ownership of core areas and linkages with protection status using the Protected Areas Database of the United States (USGS, 2018) and the Canadian Protected and Conserved Areas Database (Environment Canada, 2020), which include private conservation lands and public lands at all jurisdictional levels (Table 1; Appendix D). Only terrestrial parts of protected areas were used in analyses. We examined core area size to estimate their potential to maintain a viable population alone or with immigration, using areas of >25,600 and 12,800–25,600 km², respectively (USFWS, 1992), and defined these as population-sized core areas (PCAs).

3. Results

From the initial 3238 presence points (1601 in Minnesota, 1002 in Wisconsin, and 635 in Michigan) we created a filtered dataset of 2832 wolf presence points (1095, 1141, and 596, respectively) and 6928 pseudo-absence points (Appendix A). The proportion of natural land cover (VIF = 13.06) and agricultural land cover (VIF = 12.07) were correlated (r = −0.92) and we retained proportion of agriculture due to better model fit. No variables used in the final model with five variables had VIF > 1.82 or pairwise correlation > 0.57.

All submodels except the SRE had TSS scores ≥ 0.5 and were included in the ensemble model. The ensemble model had ROC and TSS scores of 0.87 and 0.59, respectively, and the suitability map had a sensitivity and specificity of 90.7 and 68.3, respectively. Averaged variable importance suggested proportion of agricultural cover as most influential (0.32), followed by human population density (0.22), and distance to agricultural land cover (0.15). Elevation (0.05) and distance to natural land cover (0.03) were of least importance. Our model estimated a strong decline in wolf presence likelihood at human population densities 50–75/km², and an inverse relationship with proportions of agricultural land (Appendix C).

Overall, we estimated 1,174,839 km², or 34.7 % of former range in the eastern USA (3,385,780 km²) as potential wolf habitat. Wolves currently occupy 4.1 %, or 139,462 km², of their former range, which is

Table 1
Management jurisdictions and land designations of protected areas within core areas (i.e. suitable areas > 100 km²) and linkages (i.e. 1 km buffer around least-cost paths connecting core area pairs) for gray wolves (*Canis lupus*) throughout former range in the eastern USA (Nowak, 1995).

Protected status of core areas			Protected status of linkages		
Management jurisdiction	Area (km²)	%	Management jurisdiction	Area (km²)	%
State	106,238	34.5	State	1342	35.6
Federal	104,589	34.0	Unknown	694	18.4
Land designation	33,415	10.9	Federal	537	14.2
Unknown	26,873	8.7	Private	451	12.0
Private	17,367	5.6	Land designation	391	10.4
Local government	10,824	3.5	Local government	188	5.0
Non-governmental organization	5644	1.8	Non-governmental organization	128	3.4
Other	3078	1.0	Other	42	1.1

Protected status of core areas			Protected status of linkages		
Land designation	Area (km²)	%	Land designation	Area (km²)	%
National forest	65,574	21.3	Conservation easement	825	21.9
State resource management area	55,329	18.0	State conservation area	521	13.8
State conservation area	44,808	14.6	State resource management area	502	13.3
Conservation easement	25,228	8.2	National forest	257	6.8
State wilderness	11,459	3.7	State park	222	5.9
National grassland	9550	3.1	Recreation management area	198	5.3
Local conservation area	9407	3.0	National Wildlife Refuge	180	4.8
Wilderness area	9221	3.0	Military land	147	3.9
Unknown easement	9007	2.9	Marine protected area	136	3.6
National park	7301	2.4	Private conservation	109	2.9
State park	7133	2.3	Local park	91	2.4
Other	51,256	16.6	Other	583	15.5

11.9 % of the area we estimated suitable. We identified 161 core areas comprising 1,760,835 km² overall, with the largest 5 comprising 94.8 % of the total (Fig. 2). We identified 6 population-sized core areas (PCAs) including the currently occupied Great Lakes PCA (135,060 km²). The 5 unoccupied PCAs (18,110 to 725,488 km²) included 3 which could maintain independent populations and 2 estimated as immigration-dependent (Fig. 2). Among core areas, 308,028 km² (17.5 %) had protected area status, most commonly national forests (21.3 %) (Table 1). Protected areas within PCAs were managed primarily by state (34.5 %) and federal governments (33.6 %).

We identified 242 least-cost paths (LCPs) 3.8–573.6-km long (Fig. 3), and a total linkage area of 26,871 km² in the eastern USA, of which 3887 km² (14.5 %) was within protected areas. The most common land designation for linkage protection was conservation easement (21.9 %), and protected areas within linkages were primarily state-managed (35.6 %) (Table 1). The circuit connectivity map suggested highest connectivity within the Great Plains PCA, the Great Lakes PCA, and the Appalachian PCA, and in Canada north of Lake Superior (Appendix E). Direct linkages between the Great Plains and Great Lakes PCAs have medium connectivity, while areas south of the Great Lakes PCA have low connectivity (Fig. 3). There is high connectivity between the Great

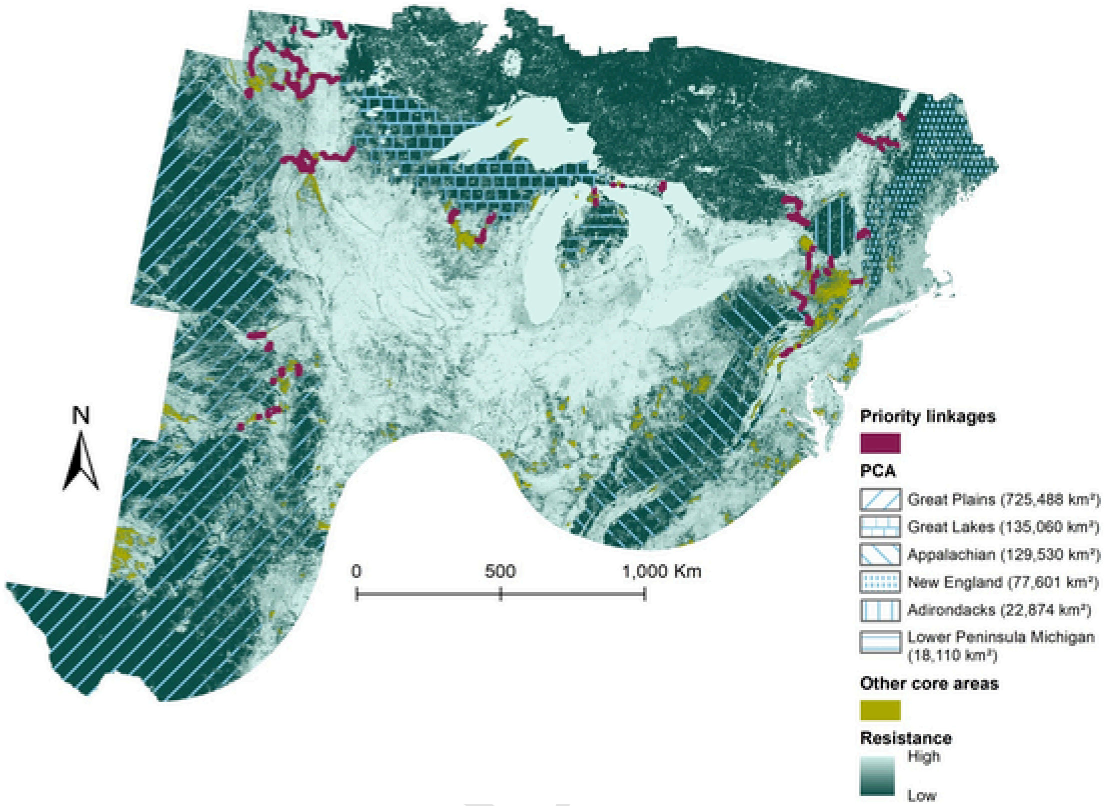

Fig. 2. Landscape resistance for gray wolves (*Canis lupus*) throughout former range in the eastern USA (Nowak, 1995) and southern Canada, and the top third linkages in terms of priority based on cost-weighted distance and qualities of core areas they connect. Landscape resistance is overlaid with core areas of habitat in the USA, including six population-sized core areas (PCAs) that could host viable wolf populations (>12,800 km^2) (USFWS, 1992).

Lakes PCA and currently occupied habitat in Canada, extending east to the St. Lawrence River.

Assuming wolves use the lowest-CWD linkage to cross from the Great Lakes PCA to a core area in central Wisconsin where wolves are present (Thiel et al., 2009; Wisconsin DNR, 2021), we consider this a baseline suitable linkage (Fig. 3). The only direct linkages between PCAs with a CWD equal to or less than this linkage is the Straits of Mackinac which connects the Great Lakes PCA with the Lower Peninsula Michigan PCA, and a linkage between the New England and Adirondacks PCAs. Four smaller core areas between Montreal and Quebec City, Canada, connect large areas of wolf habitat between Manitoba and Ontario with a larger core area east of the St. Lawrence River which in turn connects to the New England PCA. This potential route contains four short linkages with individual CWDs less than the baseline linkage.

4. Discussion

We estimated gray wolf habitat across former range in the eastern USA, supporting our prediction that wolves occupy areas with low human disturbance and high natural land cover (Mladenoff and Sickley, 1998; Smith et al., 2016). We estimated 65.3 % of former range in the eastern USA is currently unsuitable for wolves. Following USFWS criteria (USFWS, 1992), we identified 6 core areas in the eastern USA that could maintain viable wolf populations after natural recolonization or reintroduction, of which only the Great Lakes PCA (population-sized core area) is currently occupied. Overall, 17.5 % of core areas have protected status, primarily under state and federal jurisdiction. Connectivity between current wolf range and other PCAs appears limited due to extensive agriculture, high human populations, and presence of the Great Lakes. Consequently, recolonization of the three easternmost PCAs appears most plausible via dispersal through or from current wolf range in southern Canada.

Gray wolves are habitat generalists, thus climatic, geological, or biological landscape features including snow cover, elevation, or vegetation types may not strongly limit their distribution (Fechter and Storch, 2014). Habitat generalism formerly allowed wolves to occupy most of North America (Nowak, 1995) and suggests the diversity of natural landscapes in the eastern USA would not limit recolonization. Our model suggests landscape suitability for wolves is primarily limited by high human population density and extensive agriculture, with wolves occupying areas with greater proportions of natural cover. Because large parts of the eastern USA have been altered by humans (Ellis et al., 2010), we estimate only 34.7 % of former wolf range (Nowak, 1995) is currently suitable for wolves.

The Great Plains, Appalachian, and New England PCAs could likely support independent populations of wolves whereas the Adirondacks and Lower Peninsula Michigan PCAs appear dependent on connectivity with other populations. We acknowledge the criteria we used for areas required to sustain populations (see USFWS, 1992) may be conservative. We estimated 3840 km^2 of habitat for a previously disjunct wolf population in central Wisconsin established around 1993 (Thiel et al., 2009) that was at least initially dependent on connectivity with the Great Lakes PCA. Wolf populations considered viable can occupy areas 1500–3000 km^2 within protected areas in North America (Fritts and Carbyn, 1995). However, protected areas cover only 21.6 % of unoccupied PCAs, compared to 55.6 % in the Great Lakes PCA (Appendix B). Wolf territory size may be inversely related to habitat quality (Kittle et al., 2015), and habitat quality in protected areas may benefit from lesser human disturbance and greater natural cover (Bassi et al., 2015), so the minimum area requirement for maintaining a population may be greater with lower protection status and habitat quality. While human tolerance and conflict mitigation are important where humans and large carnivores co-exist, it may be particularly important for wolf recolonization and persistence in unprotected areas, which represented

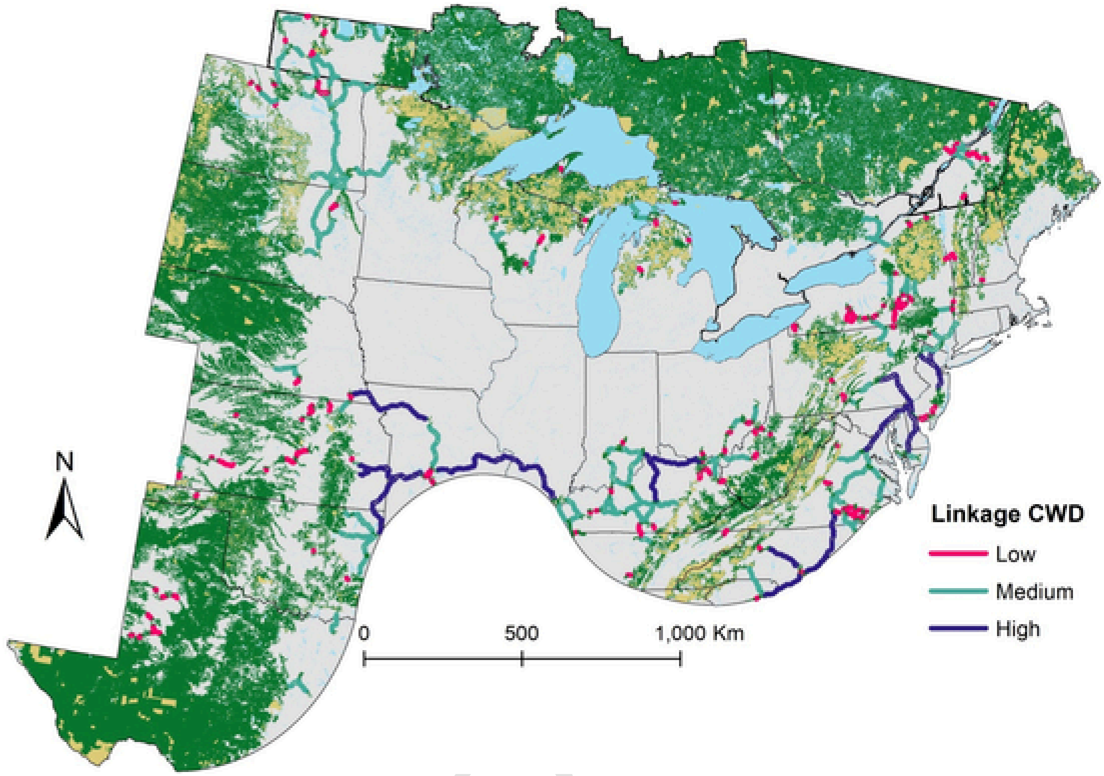

Fig. 3. Core habitat areas (i.e. suitable patch area > 100 km^2) for gray wolves (*Canis lupus*) throughout former range in the eastern USA (Nowak, 1995) and southern Canada. Core areas in dark green, intersection with protected areas in light yellow. Linkages between core areas are categorized using equal intervals of their cost-weighted distance (CWD). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

most unoccupied wolf habitat in our study (Smith et al., 2016; Gantchoff et al., 2020).

Wolves in the Great Lakes PCA can disperse >800 km in straight line distance (Michigan DNR, unpublished data), considerably greater than the longest linkage (574 km) we identified, yet typical dispersals in the Great Lakes region range from 20 to 100 km (Treves et al., 2009). Based on least-cost paths and circuit theory, we suggest the low suitability of areas connecting current wolf range with other PCAs likely limits recolonization more than linkage length does. Considering the CWD of the linkage in central Wisconsin, we suggest human disturbance and associated land use limit connectivity of many linkages within the USA, particularly in agricultural areas west and south of the Great Lakes PCA. Consequently, most linkages between current range and other PCAs incorporate areas in southern Canada, where there is reduced human disturbance (Homer et al., 2017). An exception may be the Straits of Mackinac, which could connect the Great Lakes and Lower Peninsula Michigan PCAs. Wolves can cross these straits when ice-covered, though crossings thus far appear too infrequent for population establishment (Stricker et al., 2019). Despite higher connectivity in southern Canada, human development along the St. Lawrence River may limit connectivity with the New England and Adirondacks PCAs, while anthropogenic mortality in Canada could reduce the frequency of dispersal into the eastern USA (Wydeven et al., 1998). Most linkages between current and potential range span multiple states or countries, so maintaining or improving connectivity for wolves in the eastern USA will depend on interjurisdictional cooperation, particularly in the absence of federal protection (USFWS, 2020b). Wolves were listed under the Endangered Species Act to conserve the species in "a significant portion of its range", yet controversy has arisen over the interpretation of this phrase, and whether this goal has been met (USFWS, 2020b; Defenders of Wildlife et al. v. USFWS et al., 2022). Our study provides a framework for interpreting current gray wolf range in the eastern USA in relation to potential for further recolonization and habitat loss throughout former range. Policy and management toward further recolonization of gray wolves should consider potential overlap with former range of the federally endangered red wolf (*C. rufus*) (Hinton et al., 2013).

Although further recolonization of former range by gray wolves in the eastern USA appears restricted due to limited connectivity, our estimates may be conservative because wolf populations exhibit behavioral plasticity and can select for areas previously considered unsuitable (Mladenoff et al., 2009). Species distribution and connectivity models assume species are in equilibrium with their environment, yet recolonizing species are not (Guisan and Thuiller, 2005). Our models therefore represent only the current state of wolf distribution and potential for recolonization, and future changes are difficult to predict due to variation in dispersal rates, distances, and directions (Mech and Boitani, 2003). Recolonization of current range in the Great Lakes PCA required over 30 years (Treves et al., 2009), and European countries with high habitat fragmentation and human population densities are documenting wolf re-establishment after 100–200 years of absence (Reinhardt et al., 2019; Van Der Veken et al., 2021). Further, our linkages are theoretical least-cost paths and wolves undoubtedly move through areas we have not identified. Finally, our analysis does not account for occasional long-distance dispersals over frozen lakes (e.g., Orning et al., 2020). Given the conservativeness of our analysis and unpredictability of wolf dispersal, natural recolonization beyond the Great Lakes PCA appears possible long term.

Complete prey density data for the eastern USA were unavailable, however, our model performed well in identifying suitable areas and provided output similar to previous gray wolf distribution models (Mladenoff and Sickley, 1998; Smith et al., 2016). Land cover variables, such as natural land cover used in our study, may serve as a coarse surrogate for prey density (Hanberry, 2021), on which large carnivores depend (Wolf and Ripple, 2016). Wolves are ungulate specialists and white-tailed deer (*Odocoileus virginianus*) is the primary prey of wolves in the Great Lakes PCA (DelGiudice et al., 2009). Conservative estimates suggest PCAs generally support deer densities > 5.8/km^2 (Hanberry, 2021), except the Adirondacks PCA, with typical densities ≤ 2 deer/km^2 (Hinton et al., in revision), parts of the Great Plains PCA (Hanberry, 2021), and possibly northern Maine (MDIFW, 2007). However, northern Maine has 2.7–4.0 moose (*Alces alces*)/km^2, also an important prey species for wolves (DelGiudice et al., 2009; Kantar and Cumberland, 2013). Finally, several wolf-occupied areas in the Great Lakes PCA have deer densities < 5.8/km^2 (Hanberry and Hanberry, 2020; Gable et al., 2017); low ungulate densities can result in increased use of alternative prey such as beaver (*Castor canadensis*) and smaller mammals (Newsome et al., 2016).

The suitability of areas for large carnivore recolonization depends not only on their environmental conditions, but also human willingness to co-exist with them (Treves and Karanth, 2003; Gompper et al., 2015), as recolonization can be limited by human persecution (Mech et al., 2019; Recio et al., 2020). Human tolerance depends on real and perceived risks and benefits associated with large carnivore presence (Bruskotter and Wilson, 2014). Science-based public education on wolves could aid in promoting co-existence with humans (Slagle et al., 2013; Treves and Bruskotter, 2014), while increased regulations and conflict mitigation programs may help when more direct action is required (Musiani and Paquet, 2004; Boudreau et al., 2022), particularly in rural areas where humans and wolves share landscapes and interact more frequently (Smith et al., 2014). Our results allow for prioritization of areas most likely to be reoccupied and consequently, where promoting wolf co-existence with humans is most relevant.

5. Conclusions

Despite continuing land use change, suitable areas for large carnivore recolonization remain available (Smith et al., 2016). Many of those species, such as gray wolves, cougars (*Puma concolor*), and American black bears, have recolonized former range, but only partially (Ripple et al., 2014). Nevertheless, we estimate 65 % of former wolf range in the eastern USA is currently unsuitable, and limited connectivity between occupied and unoccupied habitat may limit further wolf recolonization. Moreover, linkages for large carnivores often cross jurisdictional borders, highlighting the need for interjurisdictional cooperation if recolonization or reintroduction is desired. Our results suggest that while several parts of the eastern USA may not be recolonized naturally, there is sufficient remaining wolf habitat for reintroduction. Beyond the availability of habitat and linkages for large carnivores, their recolonization and persistence will require human willingness to share landscapes with them. Knowing where and how large carnivore recolonization may occur can aid in prioritizing areas for conservation and promoting successful co-existence with humans (Olson et al., 2021).

CRediT authorship contribution statement

M. van den Bosch: Conceptualization, Methodology, Data curation, Formal analysis, Writing - Original draft, Writing - Review & editing, Visualization

D. E. Beyer Jr.: Data curation, Writing - Review & editing, Project administration, Funding acquisition

J. D. Erb: Data curation, Writing - Review & editing, Project administration, Funding acquisition

M. G. Gantchoff: Methodology, Data curation, Writing - Review & editing

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B. R. Patterson: Methodology, Writing - Review & editing

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

The authors do not have permission to share data.

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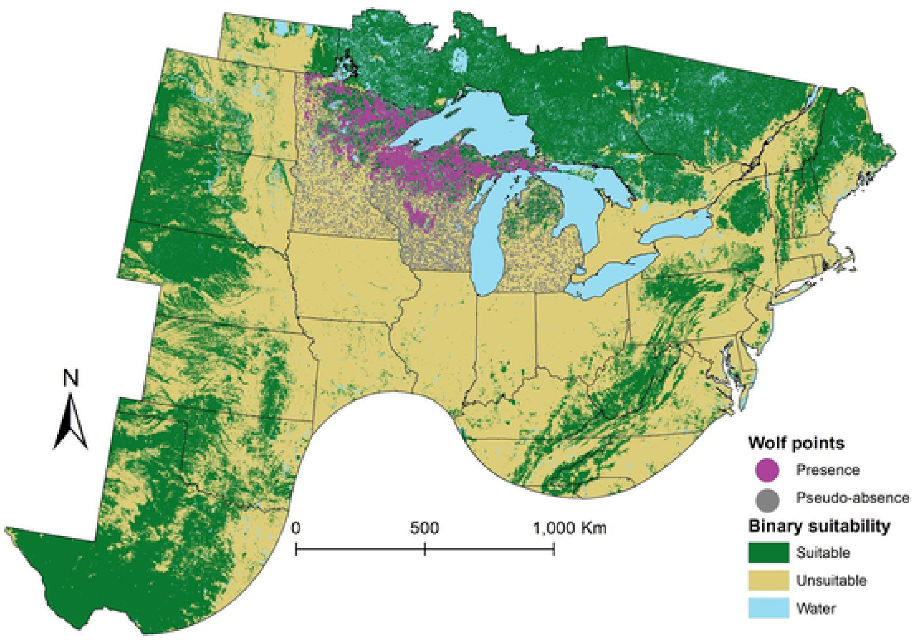
Appendix A. Binary landscape suitability for gray wolves (*Canis lupus*) throughout former range in the eastern USA (Nowak, 1995) and southern Canada, and presence and pseudo-absence points in Minnesota, Wisconsin, and Michigan, USA, used for modeling



Appendix B. Management jurisdictions and protected area land designations within gray wolf (*Canis lupus*) population-sized core areas (>12,800 km², PCAs) in the eastern USA (Nowak, 1995)

Protected status of population-sized core areas (PCAs)					
Management jurisdiction			Land designation		
Great Plains PCA	Area (km²)	%	Great Plains PCA	Area (km²)	%
Federal	49,384	64.3	State resource management area	17,984	23.4
State	24,079	31.3	Conservation easement	17,335	22.6
Non-governmental organization	2684	3.5	National grassland	9278	12.1
Local government	547	0.7	National forest	5959	7.8
Other	132	0.2	National park	4630	6.0
Total area	76,826		Other	21,640	28.1

Protected status of population-sized core areas (PCAs)					
Management jurisdiction			Land designation		
Great Lakes PCA	Area (km²)	%	Great Lakes PCA	Area (km²)	%
State	30,513	40.6	National forest	24,196	32.2
Federal	25,965	34.6	State resource management area	16,541	22.0
Local government	7976	10.6	State conservation area	13,057	17.4
Land designation	7549	10.1	Local conservation area	7745	10.3
Other	3073	4.1	Wilderness area	4208	5.6
Total area	75,076		Other	9329	12.4

Protected status of population-sized core areas (PCAs)					
Management jurisdiction			Land designation		
Appalachian PCA	Area (km²)	%	Appalachian PCA	Area (km²)	%
Federal	38,715	52.3	National forest	25,209	34.1
State	31,175	42.1	State conservation area	15,321	20.7
Joint	2351	3.2	State resource management area	13,538	18.3
Non-governmental organization	1259	1.7	Inventoried roadless area	3651	4.9
Other	506	0.7	Wilderness area	2575	3.5
Total area	74,006		Other	13,712	18.5

Protected status of population-sized core areas (PCAs)					
Management jurisdiction			Land designation		
New England PCA	Area (km²)	%	New England PCA	Area (km²)	%
Non-governmental organization	10,972	37.3	National forest	4986	16.9
Federal	9143	31.1	Unknown easement	4435	15.1
State	8682	29.5	Forest stewardship easement	3973	13.5
Local government	566	1.9	State resource management area	3561	12.1
Other	64	0.2	Conservation easement	3156	10.7
Total area	29,427		Other	9316	31.7

Protected status of population-sized core areas (PCAs)					
Management jurisdiction			Land designation		
Adirondacks PCA	Area (km²)	%	Adirondacks PCA	Area (km²)	%
State	13,968	93.5	State wilderness	9492	63.5
Non-governmental organization	443	3.0	Unknown easement	2768	18.5
Federal	374	2.5	State conservation area	1147	7.7
Local government	138	0.9	Military land	369	2.5
Other	16	0.1	State resource management area	350	2.3
Total area	14,939		Other	813	5.5

Protected status of population-sized core areas (PCAs)					
Management jurisdiction			Land designation		
Lower Peninsula Michigan PCA	Area (km²)	%	Lower Peninsula Michigan PCA	Area (km²)	%
Federal	7781	50.0	State conservation area	7370	47.3
State	7493	48.1	National forest	6920	44.5
Private	246	1.6	Military land	578	3.7
Non-governmental organization	40	0.2	Wild and scenic river	156	1.0
Other	15	0.1	Private recreation or education	125	0.8
Total area	15,574		Other	425	2.7

Appendix C. Relationship between the three most important variables of an ensemble model to predict habitat suitability for gray wolves (*Canis lupus*) in Minnesota, Wisconsin, and Michigan, USA. Submodels are listed in order of relative contribution to the ensemble model: generalized boosted model (GBM), maximum entropy (MaxEnt), artificial neural network (ANN), multivariate adaptive regression splines (MARS), generalized additive model (GAM), generalized linear model (GLM), random forest (RF), flexible discriminant analysis (FDA), classification tree analysis (CTA), and surface range envelope (SRE)

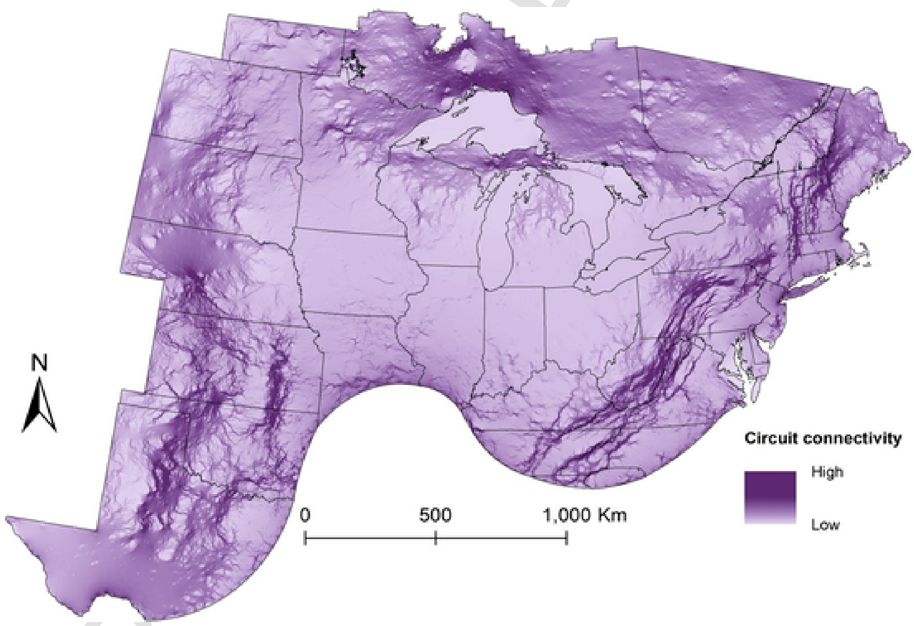
Appendix D. Management jurisdictions and protected area land designations (see Environment Canada, 2020) within gray wolf (*Canis lupus*) core areas (i.e. wolf habitat > 100 km²) and linkages throughout the Canadian portion of the study area

Protected status of core areas			Protected status of linkages		
Management jurisdiction	Area (km²)	%	Management jurisdiction	Area (km²)	%
Sub-national government	46,115	93.2	Sub-national government	84	73.7
National government	3110	6.3	National government	25	21.8
Collaborative governance	127	0.3	Non-profit organizations	4	3.8

Protected status of core areas			Protected status of linkages		
Management jurisdiction	Area (km²)	%	Management jurisdiction	Area (km²)	%
Non-profit organizations	107	0.2	Collaborative governance	1	0.7

Protected status of core areas			Protected status of linkages		
Land designation	Area (km²)	%	Land designation	Area (km²)	%
Provincial park	20,863	42.2	Wildlife management area	39	33.9
Conservation reserve	10,158	20.5	Waterfowl gathering area	23	19.9
Proposed biodiversity reserve	4543	9.2	Provincial park	21	18.4
Quebec's national park	3115	6.3	National marine park	20	17.4
National park	2620	5.3	Private land	4	3.8
Biological refuge	2233	4.5	National park	3	2.4
Proposed aquatic reserve	1614	3.3	National wildlife area	2	2.0
Biodiversity reserve	1539	3.1	Quebec's national park	2	1.4
Other	2796	5.6	Recognized nature reserve	1	0.7

Appendix E. Circuit connectivity for gray wolves (*Canis lupus*) throughout former range in the eastern USA (Nowak, 1995) and southern Canada, representing habitat connectivity for a gray wolf moving randomly through the landscape



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