**Temporal dynamics in gray wolf space use suggest stabilizing range in the Great Lakes region, USA**

**Authors**  
M. van den Boscha\*, D. E. Beyer, Jra, J. D. Erbb, M. G. Gantchoffc, K. F. Kellnera, D. M. MacFarlandd, B. R. Pattersone, J. L. Price Tackd, B. J. Roellf, J. L. Belanta

*\*Corresponding author. merijnvdb@gmail.com (M. van den Bosch), Tel: 631-487 0141.*

## **Highlights**

* Wolves occupied areas with higher human disturbance as recolonization progressed.
* Increases in areas recolonized by gray wolves have declined over time.
* Recolonization is now constrained by human disturbance, suggesting range stabilization.
* Distribution models need to acknowledge dynamic landscape use of recolonizing species.

**Abstract**

Species distribution models can facilitate conservation planning and action but presume species-environment relationships are stable, which is not the case for invasive or recolonizing species only partially occupying their potential distributions. This complicates our understanding of colonization and recolonization processes and their effects on species’ distributions. We combined snow tracking data collected during gray wolf (*Canis lupus*) recolonization of the western Great Lakes region (Minnesota, Wisconsin, Michigan, USA) into six periods during 1989–2020 and used a species distribution model to assess temporal variation in wolf distribution in response to human population density and proportion of agricultural land cover. We found negative relationships between these covariates of human disturbance and wolf habitat suitability, with the magnitude of these relationships declining over time. Estimated wolf habitat increased 35%, from 148,500 km2 in the first (1989–1994) period to about 201,000 km2 in the last (2016–2020) period, though increases in habitat declined across periods. Wolf presence was associated with increasing levels of human disturbance as recolonization progressed, demonstrating temporal variation in the relationship between wolf presence and indices of human disturbance. The western Great Lakes wolf population likely occupies most areas currently suitable and is limited by human landscape disturbances, resulting in apparent stabilization of regional wolf range.

**Keywords**

Gray wolf, species distribution, recolonization, equilibrium, space use, range stabilization

1. **Introduction**

The 21st century is characterized by an ongoing anthropogenic mass extinction event, with vertebrate extinctions having increased up to one hundredfold from historical extinction rates (Ceballos et al., 2015). Major causes of the biodiversity crisis include climate change (Thomas et al., 2004) and habitat loss and fragmentation (Fahrig et al., 2003). Species distribution models can be used to predict how species ranges could change in response to such anthropogenic environmental changes, facilitating conservation planning and action (Guisan and Thuiller, 2005). Predicting species ranges is also important to estimate potential expansion of recolonizing, reintroduced, or invasive species, whether these promote biodiversity (Ripple and Beschta, 2012) or degrade it (Clavero and García-Berthou, 2005; Lockwood et al., 2013). Informed forecasts of species’ invasion, colonization, or recolonization can therefore help to mitigate or effectuate range shifts (Mladenoff and Sickley, 1998; Jiménez-Valverde et al., 2011). Unraveling mechanisms influencing colonization or recolonization includes understanding the species’ realized niche, the environmental space a species occupies as limited by environmental factors, through modeling relationships between species occurrences and environmental variables (Guisan et al., 2017). However, these models presume species-environment relationships are stable (Guisan and Zimmermann, 2000; Elith and Leathwick, 2009), which rarely occurs for invasive (Václavík and Meentemeyer, 2012), reintroduced, or recolonizing species (Svenning and Skov, 2004) that often only partially occupy their potential distribution and are not in spatial equilibrium with their environment (Guisan and Thuiller, 2005). Using species distribution models developed from presence data that do not represent the full range of suitable conditions for a species in an area can reduce model accuracy and usefulness (Václavík and Meentemeyer, 2012). However, the extent to which violating the assumption of a species-environment equilibrium impacts the results of static species distribution models is largely unknown.

Large carnivores are recolonizing parts of their historical range in North America (Gompper et al., 2015) and Europe (Chapron et al., 2014). Partial recolonizations of historical carnivore ranges resulted from increased legal protection of carnivores and their habitat, and changing public perception (Chapron et al., 2014; Gompper et al., 2015). However, human presence and disturbance remains the most limiting factor of carnivore distributions in human-dominated landscapes (Laliberte and Ripple, 2004; Smith et al., 2016; Wolf and Ripple, 2017). Gray wolves (*Canis lupus*) once occupied most of the conterminous United States but were largely extirpated by 1970 (Boitani, 2003). Following federal protection in 1974 through the United States Endangered Species Act (ESA), wolves recolonized large portions of the western Great Lakes region of the USA (Mladenoff et al., 2009). In addition to federal protection, recolonization was facilitated by adequate prey populations (DelGiudice et al., 2009). The western Great Lakes population has recently stabilized at around 4,200 wolves, more recently for Michigan (2011) and Wisconsin (2017) than for Minnesota (2005 or earlier; USFWS, 2020). Wolf recolonization could be spatially constrained by anthropogenic disturbances and mortality risk (Mech, 2017; Hill et al., 2022). Earlier research identified negative relationships between wolf habitat suitability and indices of human disturbance (Mladenoff et al., 1995; Carroll et al., 2003; [Martínez-Meyer](https://onlinelibrary.wiley.com/authored-by/Mart%C3%ADnez%E2%80%90Meyer/Enrique) et al., 2021), and habitat suitability for wolves in the Great Lakes region strongly declines with increasing agricultural activities and human population densities (van den Bosch et al., 2022), likely because of the perceived and real risks of human presence and activities to wolves (Oriol-Cotterill et al., 2015). Nevertheless, previous studies may have underestimated limits of wolf tolerance for human disturbance (Mladenoff et al., 1995; Mladenoff and Sickley, 1998, Carroll et al., 2003) by not accounting for wolves occupying an incomplete realized niche (Mladenoff et al., 2009; O’Neil et al., 2019). In Minnesota (Mech, 1989) and Wisconsin (Mladenoff et al., 2009) wolves occupied areas with lower road densities before their legal protection in 1974 than after (Thiel et al., 1985; Mech, 1989), and continued to occupy areas with higher road densities in the early 2000s (Mladenoff et al., 2009). Temporally dynamic landscape use by the western Great Lakes region wolf population during recolonization complicates our understanding of their potential distribution.

We used observational wolf winter survey data collected during 1989–2020 to assess temporal variation in wolf distribution in response to landscape characteristics in the western Great Lakes region, USA. We predicted wolves would increasingly occupy areas with greater human disturbance, represented by agricultural land cover and human population densities, during recolonization and range expansion. We also predicted a decreasing rate of recolonized habitat and that wolves currently occupy most available suitable areas.

1. **Methods**

*2.1 Study area*

The western Great Lakes region (Figure 1) comprises the states of Minnesota (220,185 km2), Wisconsin (145,594 km2), and Michigan (150,648 km2), USA. This region is dominated by forest (44%) in the north and agricultural land (37%) in the south, with 86% of the area within 10 km of natural water features (NLCD, 2016; Gantchoff et al., 2021). Elevations are 174–701 meters above sea level (USGS, 1996). Human population densities are > 100 km2 in the southern part of each state and decrease substantially along a south-north gradient (US Census Bureau, 2010; NLCD, 2016).  
 The western Great Lakes wolf population in 1974 comprised about 750 individuals in northeastern Minnesota and a small population on Isle Royale, Michigan (Erb and DonCarlos, 2009). Legal protection and deer population recovery facilitated population growth in Minnesota, resulting in the recolonization of northern Wisconsin by 1975 (Wydeven et al., 2009) and the Upper Peninsula of Michigan by 1989 (Beyer et al., 2009). Recent estimates of wolf population size are about 4,200 individuals, with 2,600 in Minnesota, 900 in Wisconsin, and 700 in the Upper Peninsula of Michigan (USFWS, 2020).

*2.2 Data collection* We used winter survey data on gray wolves collected by the Departments of Natural Resources (DNR) of Minnesota, Wisconsin, and Michigan during 1989–2020. In Minnesota, trained natural resource officers were instructed to record locations of all wolf sightings and signs (e.g., tracks, scat) observed during work hours from November until snowmelt, usually mid-May (Erb and Sampson, 2013; Gantchoff et al., 2022). Participants could record locations on forms or maps, but more recently primarily used a web-based GIS application. The final datasets were combined with other presence data recorded during other surveys coordinated by the DNR (e.g., furbearer survey, carnivore scent station survey). In Wisconsin, staff 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 about 500 km²; delineated using waterways, roads, and state boundaries; ensuring each block could be surveyed within a day. Employees of the DNR, tribal biologists, and trained volunteers attempted to survey most snow-covered roads within a block 1–3 days after snowfall. In the Upper Peninsula of Michigan, surveys were conducted along roads and trails using truck or snowmobile (Michigan Department of Natural Resources, 2008) by Michigan DNR and USDA Wildlife Services staff. Survey efforts to estimate wolf abundance began in 1989 and initially emphasized areas with reported wolf sign observed by MDNR staff and the public and searching areas where wolf packs occurred in the 1940s–1950s. By 1995, staff surveyed suitable habitat across the Upper Peninsula and during 2000–2006, at least 25% of available roads and trails were surveyed at least once annually. Due to increasing wolf abundance, the Upper Peninsula was divided into 21 survey units of which 12–13 were randomly selected and surveyed annually during 2007–2011 and 2013–2014, then every other year starting 2016, ensuring ≥ 60% coverage of the Upper Peninsula. Portions of the Lower Peninsula of Michigan were periodically monitored for wolf occurrence based on reported sightings, but there were no systematic surveys as wolves have not established there (Beyer et al., 2009).

Sampling area and methodology varied across states and during the period of data collection, though we are confident sampling consistently represented the approximate distribution of wolves in each state. Monitoring in Minnesota was well-established in 1989 as wolves were not extirpated, while the approximate distribution of wolves in Wisconsin and Michigan was well-known in early years of data collection, based on public sightings and extensive agency work resulting from high public interest in wolves.

*Data selection and processing* Because areas surveyed by states varied across years, we combined data into six periods (1989–1994, 1995–2000, 2001–2005, 2006–2010, 2011–2015, and 2016–2020) that represented the shortest intervals during which complete spatial coverage of the study area was obtained. To account for spatial autocorrelation, we filtered each dataset to a maximum of one presence point per 3-km2 cell (Guisan et al., 2017 van den Bosch et al., 2022) and randomly generated two pseudo-absence points for each presence point, ensuring presence and pseudo-absence points by period did not co-occur within a cell (Barbet-Massin et al., 2012; Guisan et al., 2017). We excluded Isle Royale National Park, Michigan, as we had no survey data. We chose random sampling despite potential sampling bias (Phillips et al., 2009) because the regional distribution of wolves was well-known from monitoring during the period of data collection.

*2.3 Modeling* To model temporal relationships between wolf habitat suitability and human landscape disturbances, we used National Land Cover Databases (30-m resolution) (Yang et al., 2016; Dewitz, 2019; NLCD, 2001; 2006; 2008; 2011; 2016; 2020) to derive proportions of agricultural land cover (classes planted/cultivated and pasture/hay) (Figure 1), and layers of human population density (per km2) from 5 yearly Gridded Population of the World V4.11 (30 arc-second resolution) datasets (CIESIN, 2000; 2005; 2010; 2015; 2020). We extracted variables from the respective datasets most temporally aligned with each period of data collection. As the earliest and most recent datasets were highly correlated for proportion of agricultural land cover (*r* = 0.97) and human population density (*r* = 0.98), we assumed similarity of these metrics in earlier years and used values from the 2000 dataset for periods for which data were unavailable. We rescaled covariates to 3-km resolution to reduce spatial mismatch between species data and our covariates (Guisan and Thuiller, 2005). This was the finest possible resolution as data contained presence points collected with accuracy to the nearest mile (1.61 km). We removed cells classified as water from analysis then scaled continuous variables (-1 to 1) to facilitate effect size comparison. We did not use variables related to developed land cover (e.g. road density, proportion of developed cover, etc.) as surveys were conducted along roads which causes positive bias between wolf presence and such variables (van den Bosch et al., 2022). However, we plotted primary roads (US Census Bureau, 2020) on maps showing habitat predictions to interpret these as potential barriers to range expansion. We used variance inflation factors (VIF) and pairwise correlations to test for multicollinearity between variables. We created two models when covariates had pairwise correlations > 0.70, each with one of the correlated variables, and removed the variable resulting in a greater AIC score from the final model (Burnham and Anderson, 2003; Guisan et al., 2017).

We used a binomial generalized linear model in program R 3.6.2 (R Core Team, 2020), with proportion of agricultural land cover and human population density as continuous variables which were not correlated (*r* =-0.09– -0.10 across six periods), and interactions of these variables with the six periods of data. A binomial generalized linear model employs a binary response variable (0/1), thus can be used as a species distribution model by using species presences (= 1) and pseudo-absences (= 0) as the response variable (Guisan et al., 2017). We used the area under the curve (AUC) of the receiver-operating characteristic (ROC), along with associated sensitivity and specificity scores, to evaluate model performance. We considered scores of AUC ≥ 0.90 as excellent, 0.90 > x ≥ 0.80 as good and 0.80 > x ≥ 0.70 as fair (Araújo et al., 2005). We used the DHARMa package in R (Hartig et al., 2017) to assess model fit diagnostics by testing for data dispersion, distribution, and outliers.

To assess temporal dynamics in wolf distribution we created binary habitat predictions for each period. We transformed habitat suitability maps for each period to binary format (i.e., suitable or unsuitable) by defining a threshold suitability that maximized sensitivity and specificity per period, using the ROCR package in R (Sing et al., 2005; Guisan et al., 2017). We then estimated total habitat area for each period. To quantify uncertainty associated with habitat area estimates, we used a bootstrap approach which incorporated random variability in the selection of pseudo-absence points and uncertainty around the model parameter estimates. We ran 1,000 bootstrap simulations, whereby each simulation fit a model using a randomly generated set of pseudo-absence points. From each fitted model, we randomly sampled a set of parameter estimates based on the point estimates and associated variance-covariance matrices. We used these estimates to predict habitat suitability. This bootstrap approach yielded a distribution of total habitat area for each period, from which we calculated a 95% confidence interval.

We used response curves of continuous variables to indicate effects on habitat suitability for each period (Elith et al., 2005), and binary habitat suitability maps to illustrate where the bootstrapped model predicted unchanged, gained, or lost habitat between the first and last period (Thuiller et al., 2009). An overall reduction in the rate of increase in estimated wolf habitat across periods would suggest the wolf population is approaching spatial equilibrium. We conducted a post-hoc evaluation of mean road densities in gained or lost wolf habitat between periods to compare our results to previous studies (Thiel, 1985; Mech, 1989, Mladenoff et al., 2009).

1. **Results**

The number of presence points for the six periods were 542 (1989–1994), 1253 (1995–2000), 1163 (2001–2005), 1584 (2006–2010), 1608 (2011–2015), and 1588 (2016–2020) (Appendix A). Our species distribution model had good model performance (AUC = 0.82). There were no indications of poor model fit relating to data dispersion, distribution, or outliers (Appendix B). Our model indicated negative relationships between habitat suitability and human population density, and between habitat suitability and proportional agricultural land cover (Table 1, Figure 2). The negative relationship between habitat suitability and human population density was stronger in the first (1989–1994) period than in the fourth (2006–2010), fifth (2011–2015), and sixth (2016–2020) periods. The negative relationship between habitat suitability and proportional agricultural land cover was stronger in the first (1989–1994) period than in the fifth (2011–2015) and sixth (2016–2020) periods. Overall, the strength of negative relationships between habitat suitability and these covariates decreased over time, particularly for human population density.

Our binary habitat classification estimated about 148,500 km2 of wolf habitat in the first (1989–1994) period, increasing 35% to about 201,000 km2 by the last (2016–2020) period (Figure 3). Estimated wolf habitat increased between periods except between the second (1995–2000) and third (2001–2005) periods and increases in habitat overall slowed across periods. Habitat gains occurred primarily in the periphery of occupied wolf range, whereas minimal habitat losses (500 km2; 0.003%) were dispersed throughout wolf range (Figure 4). Mean road densities were greater in predicted habitat gained between the fifth (2011–2015) and last (2016–2020) period (1.44 km/km2) than in habitat present in the first period (1989–1994; 0.87 km/km2). Finally, primary limited-access roads such as interstate highways were predominantly found in areas outside of past and current wolf range.

1. **Discussion**

We identified negative relationships between gray wolf habitat suitability in the Great Lakes region and two indices of human disturbance, human population density and proportions of agricultural land cover, supporting our prediction (Table 1; Figure 2). Our prediction of wolves expanding their range to include areas with higher human disturbance was also supported (Figure 4). We estimated a 35% increase in wolf habitat between the first (1989–1994) and last (2016–2020) periods (Figure 3). However, wolf range expansion into areas with more human disturbance appeared to slow during more recent periods, most notably in response to human population density (Figure 2), indicating wolves may be approaching the maximum extent of recolonization within the study area (Figure 3). If wolves are near spatial equilibrium, we can infer the approximate upper thresholds of human disturbance that wolves can tolerate in the western Great Lakes region. For example, using wolf presence locations from habitat gained between the last (2016–2020) and preceding (2011–2015) periods, mean proportions of agriculture were 20.73/100 and human population densities were 11.40/km2.

Gray wolves in the Great Lakes region have expanded their range from relatively undisturbed areas of northeastern Minnesota to include areas of the Great Lakes region with higher human landscape disturbance, whereby maximum road densities of occupied areas increased from 0.53 km/km2 during 1926–1960 (Thiel, 1985) to 0.73 km/km2 during 1969–1986 (Mech, 1989) and 0.93 km/km2 in 2007 (Mladenoff et al., 2009). This increased use of areas with higher human disturbance has continued, given the greater mean road densities in habitat gained during 2016–2020 (1.44 km/km2).

We note several limitations of our study. Large carnivore presence depends on prey availability (Wolf and Ripple, 2016), but prey density data within our study area for the period of inference were unavailable. Yet there are several reasons supporting the reliability of our results. Firstly, our model had overall good performance and its results for the most recent period (2016–2020) align well with previous research in this study area which differed in methodology and included other variables (Smith et al., 2016; van den Bosch et al., 2022). Secondly, land cover is a coarse surrogate for prey availability, as in our study area densities of white-tailed deer (*Odocoileus virginianus*; the primary prey of wolves) are positively correlated with high natural cover and negatively correlated with high agricultural cover (Hanberry et al., 2021). Finally, while deer are the primary prey of wolves in the study area, they are dietary generalists that can use alternative prey such as beavers (*Castor canadensis*) and other smaller mammals when there is low ungulate availability (Newsome et al., 2016; Gable et al., 2018). Our model predicted a decrease in wolf habitat in the third (2001–2005) period compared to the second (1995–2000), apparently related to a temporarily increased negative relationship between habitat suitability and proportions of agricultural land cover. This was presumably caused by an unknown bias, potentially related to sampling effort or changes in sampling protocol, as the strength of the negative relationship between habitat suitability and human population density otherwise decreased across periods. Finally, the relationship between wolf habitat suitability and proportions of agricultural land cover could vary among regions. For example, in other areas agricultural land can be further from human residences, potentially reducing the perceived anthropogenic risk for wolves (Bradley and Pletscher, 2010).

The western Great Lakes region wolf population expanded rapidly in numbers from its legal protection in 1974 until the period 2000–2010, after which population growth decreased markedly (USFWS, 2020). Though our estimates of wolf habitat area continued to increase after 2010, the magnitude of change declined overall across periods and suggests that along with a stabilizing wolf population, the rate of wolf range expansion within the Great Lakes region has slowed. Most areas estimated to be currently unsuitable for wolves have markedly higher levels of human disturbance than currently occupied areas, and primary roads are more prevalent within areas predicted to be unsuitable. While parts of the northern Lower Peninsula of Michigan have relatively low human disturbance it has not been recolonized. Although wolves have crossed to the Lower Peninsula on several occasions (Wheeldon, Patterson & Beyer 2012), the Straits of Mackinaw limit dispersal due to periods of limited or no ice formation and because ships disrupt ice cover (Stricker et al., 2019; van den Bosch et al., 2022). The next closest area suitable for recolonization in the USA is in western North Dakota and South Dakota, but connectivity to this area is limited due to high human disturbance surrounding current wolf range in Minnesota (van den Bosch et al., 2022). While the upper thresholds of human disturbance wolves can co-exist with are ultimately unknown, most areas suitable for recolonization within the western Great Lakes region appear occupied, suggesting the wolf population is approaching spatial equilibrium. This stage of equilibrium occurred about 30 years following initial wolf recolonization in the region, demonstrating the importance of long-term planning in wolf and other large carnivore management during recolonization of historical range.

1. **Conclusions**

Gray wolves have increasingly occupied areas with higher levels of human disturbance during recolonization in the western Great Lakes region, but the increase in area recolonized by wolves has declined since about 2006–2010. Due to temporal variation in the relationship between environmental variables and the occurrence of a recolonizing species, dynamic landscape use of recolonizing species needs to be considered during development and interpretation of species distribution models. Further wolf recolonization of the western Great Lakes region appears largely constrained by human disturbances, potentially resulting in range stabilization. This information can aid policymakers and managers to determine the course of wolf conservation and management within and beyond the western Great Lakes region.

1. **Tables and figures**

|  |  |  |  |
| --- | --- | --- | --- |
| ***Parameter*** | ***Estimate*** | ***SE*** | ***P-value*** |
| Intercept | -2.2543 | 0.1682 | **< 0.001** |
| Prop. agriculture | -2.0428 | 0.1550 | **< 0.001** |
| Prop. agriculture : 1995–2000 | 0.188 | 0.1838 | 0.306 |
| Prop. agriculture : 2001–2005 | -0.1326 | 0.1956 | 0.498 |
| Prop. agriculture : 2006–2010 | 0.2642 | 0.1728 | 0.126 |
| Prop. agriculture : 2011–2015 | 0.5146 | 0.1696 | **0.002** |
| Prop. agriculture : 2016–2020 | 0.6113 | 0.1667 | **< 0.001** |
| Human pop. dens. | -2.2409 | 0.4348 | **< 0.001** |
| Human pop. dens. : 1995–2000 | 0.3042 | 0.4990 | 0.542 |
| Human pop. dens. : 2001–2005 | 0.9128 | 0.4719 | 0.053 |
| Human pop. dens. : 2006–2010 | 1.4636 | 0.4456 | **0.001** |
| Human pop. dens. : 2011–2015 | 1.5026 | 0.4414 | **< 0.001** |
| Human pop. dens. : 2016–2020 | 1.6081 | 0.4416 | **< 0.001** |

**Table 1.** Results from a binomial generalized linear model comparing gray wolf (Canis lupus) presences and pseudo-absences within the Great Lakes region, USA, 1989–2020. Variables included proportion of agricultural land cover (Prop. agriculture), human population density (Human pop. dens., per km2), and their interaction with six periods of data (reference level: first period = 1989–1994). Continuous variables were scaled (-1 to 1), parameter estimates are reported with standard error (SE) and p-values (α < 0.05).



**Figure 1.** Land cover in Minnesota, Wisconsin, and Michigan, USA including the adjacent Great Lakes (from National Land Cover Database 2019).

**Figure 2.** Relationship between predicted habitat suitability for gray wolves (*Canis lupus*) and human population density (per km2, left panel) and proportion of agriculture (%, right panel) including 95% confidence intervals (shaded) in Minnesota, Wisconsin, and Michigan, USA, 1989–2020.

 **Figure 3.** Change in predicted habitat (km2) for gray wolves (*Canis lupus*) in Minnesota, Wisconsin, and Michigan, USA, 1989–2020. Confidence intervals are 95% and were obtained using a bootstrap approach.

**A map of the united states

Description automatically generated**

**Figure 4.** Predicted change in estimated habitat for gray wolves (*Canis lupus*) in Minnesota, Wisconsin, and Michigan, USA, between 1989−1994 and 2016−2020. Primary roads were derived from the TIGER/line shapefile database and are limited-access highways such as interstate highways (US Census Bureau, 2020).



**Appendix A.** Density contours of wolf presence points collected by period used to model the relationship between anthropogenic disturbances and gray wolf (*Canis lupus*) habitat suitability in Minnesota, Wisconsin, and Michigan, USA, 1989–2020. Darker colors indicate lower, and brighter colors indicate higher, point densities.

**Appendix B.** DHARMa residual tests for a binomial generalized linear model to predict the relationship between anthropogenic disturbances and gray wolf (*Canis lupus*) habitat suitability in Minnesota, Wisconsin, and Michigan, USA, 1989–2020.

1. **Acknowledgements**

We thank individuals from the respective government agencies and the public that assisted with data collection.

1. **Funding**

Primary funding for manuscript preparation was provided by the U.S. Fish and Wildlife Service through the Great Lakes Fish and Wildlife Restoration Act and Boone and Crockett Program at Michigan State University.

1. **Bibliography**

Araújo, M.B., Pearson, R.G., Thuiller, W., Erhard, M., 2005. Validation of species-climate impact models under climate change. Glob. Chang. Biol. 11, 1504–1513. <https://doi.org/10.1111/j.1365-2486.2005.01000.x>

Barbet‐Massin, M., Jiguet, F., Albert, C.H., Thuiller, W., 2012. Selecting pseudo‐absences for species distribution models: How, where and how many?. Methods Ecol. Evol. 3. 327–338. <https://doi.org/10.1111/j.2041-210X.2011.00172.x>

Beyer, D.E., Peterson, R.O., Vucetich, J.A., Hammill, J.H, 2009. Wolf population changes in Michigan. In: Wydeven, A.P., Van Deelen, T.R., Heske, E. (Eds.), Recovery of gray wolves in the Great Lakes region of the United States. Springer, New York, NY, pp. 65–85. http://doi.org/10.1007/978-0-387-85952-1\_5

Boitani, L., 2003. Wolf conservation and recovery. In: Mech, M. and Boitani, L. (Eds.), Wolves: behavior, ecology, and conservation. University of Chicago Press, Chicago, IL, pp. 317–341. <https://doi.org/10.14430/arctic540>

Bradley, E.H., Pletscher, D.H., 2005. Assessing factors related to wolf depredation of cattle in fenced pastures in Montana and Idaho. Wildl. Soc. Bull., 33, 1256–1265. [https://doi.org/10.2193/0091-7648(2005)33[1256:AFRTWD]2.0.CO;2](https://doi.org/10.2193/0091-7648(2005)33%5b1256:AFRTWD%5d2.0.CO;2)

Burnham, K.P., Anderson, D.R., 2004. Model selection and multimodel inference: a practical information-theoretic approach. Springer, New York, NY. https://doi.org/10.1007/b97636

Carroll, C., Phillips, M.K., Schumaker, N.H., Smith, D.W., 2003. Impacts of landscape change on wolf restoration success: planning a reintroduction program based on static and dynamic spatial models. Conserv. Biol. 17, 536–548. https://doi.org/10.1046/j.1523-1739.2003.01552.x

Ceballos, G., Ehrlich, P.R., Barnosky, A.D., García, A., Pringle, R.M., Palmer, T.M., 2015. Accelerated modern human–induced species losses: Entering the sixth mass extinction. Sci. Adv. 1, e1400253. <https://doi.org/10.1126/sciadv.1400253>.

Chapron, G., Kaczensky, P., Linnell, J.D.C., von Arx, M., Huber, D., Andrén, H., López-Bao, J.V., Adamec, M., Álvares, F., Anders, O., … , D., Boitani, L., 2014. Recovery of large carnivores in Europe’s modern human-dominated landscapes. Science 346, 1517–1519. <https://doi.org/10.1126/science.1257553>

CIESIN, 2020. Gridded population of the world, version 4 (GPWv4.11): population density adjusted to match 2015 revision of UN WPP country totals, revision 11. <https://doi.org/10.7927/H4F47M65>.

Clavero, M., García-berthou, E., 2005. Invasive species are a leading cause of animal extinctions. Trends Ecol. Evol. 20, 110–110. https://doi.org/10.1016/j.tree.2005.01.003

Darimont, C.T., Paquet, P.C., 2002. Gray wolves, Canis lupus, of British Columbia's central and north coast: distribution and conservation assessment. Can. Field-Nat. 116, 416–422.

Defenders of Wildlife et al v. U.S. Fish and Wildlife Service et al., 2022. No. 21-CV-00344-JSW, 2022 WL 499838 (N.D. Cal. Feb. 10, 2022). United States District Court, Northern District of California. Available at: <https://biologicaldiversity.org/species/mammals/pdfs/Wolf-Order-2022-02-10.pdf>

Dewitz, J., 2019, National Land Cover Database (NLCD) 2016 Products: U.S. geological survey data release. https://doi.org/10.5066/P96HHBIE.

Elith, J., Ferrier, S., Huettmann, F., Leathwick, J., 2005. The evaluation strip: a new and robust method for plotting predicted responses from species distribution models. Ecol. Modell. 186, 280–289. <https://doi.org/10.1016/j.ecolmodel.2004.12.007>

Elith, J., & Leathwick, J. R. (2009). Species distribution models: ecological explanation and prediction across space and time. Annu. Rev. Ecol. Evol. Syst.  40, 677–697. <https://doi.org/10.1146/annurev.ecolsys.110308.120159>

Erb, J., DonCarlos, M.W., 2009. An overview of the legal history and population status of wolves in Minnesota. In: Wydeven, A.P., Van Deelen, T.R., Heske, E. (Eds.), Recovery of gray wolves in the Great Lakes region of the United States. Springer, New York, NY, pp. 49–64. http://doi.org/10.1007/978-0-387-85952-1\_4

Erb, J., Sampson, B., 2013. Distribution and abundance of wolves in Minnesota, 2012–13. Minnesota Department of Natural Resources. Available at: http://files.dnr.state.mn.us/fish\_wildlife/wildlife/wolves/2013/wolfsurvey\_2013.pdf

Fahrig, L., 2003. Effects of habitat fragmentation on biodiversity. Annu. Rev. Ecol. Evol. Syst. 34, 487–515. https://doi.org/10.1146/annurev.ecolsys.34.011802.132419

Fechter, D., Storch, I., 2014. How many wolves (Canis lupus) fit into Germany? The role of assumptions in predictive rule-based habitat models for habitat generalists. PloS one 9, e101798. <https://doi.org/10.1371/journal.pone.0101798>

Gable, T.D., Windels, S.K., Romanski, M.C., Rosell, F., 2018. The forgotten prey of an iconic predator: a review of interactions between grey wolves Canis lupus and beavers Castor spp. Mamm. Rev., 48, 123–138. <https://doi.org/10.1111/mam.12118>

Gantchoff, M.G., Erb, J.D., MacFarland, D.M., Norton, D.C., Price Tack, J.L., Roell, B.J., Belant, J.L., 2021. Potential distribution and connectivity for recolonizing cougars in the Great Lakes region, USA. Biol. Conserv. 257, 109144. <https://doi.org/10.1016/j.biocon.2021.109144>

Gantchoff, M. G., Beyer Jr, D. E., Erb, J. D., MacFarland, D. M., Norton, D. C., Roell, B. J., ..., Belant, J. L., 2022. Distribution model transferability for a wide-ranging species, the Gray Wolf. Sci. Rep. 12, 13556.

Gompper, M.E., Belant, J.L., Kays, R., 2015. Carnivore coexistence: America’s recovery. Science 347, 382–383. https://doi.org/10.1126/science.347.6220.382-b

Guisan, A., Thuiller, W., 2005. Predicting species distribution: offering more than simple habitat models. Ecol. Lett. 8, 993–1009. https://doi.org/10.1111/j.1461-0248.2005.00792.x

Guisan, A., Thuiller, W., Zimmermann, N.E., 2017. Environmental predictors: issues of processing and selection, in: Habitat Suitability and Distribution Models. Cambridge University Press, Cambridge, pp. 61–109. https://doi.org/10.1017/9781139028271.011

Guisan, A., Thuiller, W., Zimmermann, N.E., 2017. Species data: Issues of acquisition and design, in: Habitat Suitability and Distribution Models. Cambridge University Press, Cambridge, pp. 110–134. https://doi.org/10.1017/9781139028271.012

Guisan, A., Zimmermann, N.E., 2000. Predictive habitat distribution models in ecology. Ecol. Modell. 135, 147–186. <https://doi.org/10.1016/S0304-3800(00)00354-9>

Hanberry, B.B., 2021. Addressing regional relationships between white‐tailed deer densities and land classes. Ecol. Evo., 11, 13570–13578. <https://doi.org/10.1002/ece3.8084>

Hill, J.E., Boone, H.M., Gantchoff, M.G., Kautz, T.M., Kellner, K.F., Orning, …, Belant, J.L., 2022. Quantifying anthropogenic wolf mortality in relation to hunting regulations and landscape attributes across North America. Ecol. Evol. 12, e8875. https://doi.org/10.1002/ece3.8875

Jiménez-Valverde, A., Peterson, A.T., Soberón, J., Overton, J.M., Aragón, P., Lobo, J.M., 2011. Use of niche models in invasive species risk assessments. Biol. Invasions 13, 2785–2797. https://doi.org/10.1007/s10530-011-9963-4

Laliberte, A.S., Ripple, W.J., 2004. Range contractions of North American carnivores and ungulates. Bioscience. [https://doi.org/10.1641/0006-3568(2004)054[0123:RCONAC]2.0.CO;2](https://doi.org/10.1641/0006-3568(2004)054%5b0123:RCONAC%5d2.0.CO;2)

Lockwood, J.L., Hoopes, M.F., Marchetti, M.P., 2013. Invasion ecology. Wiley and Sons, New Jersey, NJ.

Martínez‐Meyer, E., González‐Bernal, A., Velasco, J.A., Swetnam, T.L., González‐Saucedo, Z.Y., Servín, J., ..., Heffelfinger, J.R., 2021. Rangewide habitat suitability analysis for the Mexican wolf (Canis lupus baileyi) to identify recovery areas in its historical distribution. Divers. Distrib. 27(4), 642–654. <https://doi.org/10.1111/ddi.13222>

Mech, L.D., 1989. Wolf population survival in an area of high road density. Am. Midl. Nat. 121, 387–389. https://doi.org/10.2307/2426043

Mech, L.D., 2017. Where can wolves live and how can we live with them? Biol. Conserv. 210, 310–317. https://doi.org/10.1016/j.biocon.2017.04.029

Michigan Department of Natural Resources (2008). Estimating wolf abundance in Michigan. Available at: http://www.mich.gov/documents/dnr/Estimating\_Wolf\_Abundance\_in\_Michigan\_060208\_239125\_7.pdf

Mladenoff, D.J., Clayton, M.K., Pratt, S.D., Sickley, T.A., Wydeven, A.P., 2009. Change in occupied wolf habitat in the northern Great Lakes region. In: Wydeven, A.P., Van Deelen, T.R., Heske, E. (Eds.), Recovery of Gray wolves in the Great Lakes region of the United States. Springer, New York, pp. 119–138. https://doi.org/10.1007/978-0-387-85952-1\_8

Mladenoff, D.J., Sickley, T.A., Haight, R.G., Wydeven, A.P., 1995. A regional landscape analysis and prediction of favorable gray wolf habitat in the northern Great Lakes region. Conserv. Biol. 9, 279–294. https://doi.org/10.1046/j.1523-1739.1995.9020279.x

Mladenoff, D., Sickley, T.A., 1998. Assessing potential gray wolf restoration in the northeastern United States : A spatial prediction of favorable habitat and potential population levels. J. Wildl. Manage. 62, 1–10. https://doi.org /[10.2307/3802259](https://doi.org/10.2307/3802259)

Newsome, T.M., Boitani, L., Chapron, G., Ciucci, P., Dickman, C.R., Dellinger, J.A., ..., Ripple, W.J., 2016. Food habits of the world's grey wolves. Mamm. Rev., 46, 255–269. <https://doi.org/10.1111/mam.12067>

O’Neil, S.T., Beyer, D.E., Bump, J.K., 2019. Territorial landscapes: incorporating density-dependence into wolf habitat selection studies. R. Soc. Open Sci. 6, 190282. <https://doi.org/10.1098/rsos.190282>

Oriol‐Cotterill, A., Valeix, M., Frank, L.G., Riginos, C., Macdonald, D.W., 2015. Landscapes of coexistence for terrestrial carnivores: the ecological consequences of being downgraded from ultimate to penultimate predator by humans. Oikos, 124, 1263–1273. <https://doi.org/10.1111/oik.02224>

Orning, E.K., Romanski, M.C., Moore, S., Chenaux-Ibrahim, Y., Hart, J., Belant, J.L., 2020. Emigration and first-year movements of initial wolf translocations to Isle Royale. Northeast. Nat. 27, 701–708. https://doi.org/10.1656/045.027.0410

Phillips, S.J., Dudík, M., Elith, J., Graham, C.H., Lehmann, A., Leathwick, J., Ferrier, S., 2009. Sample selection bias and presence-only distribution models: implications for background and pseudo-absence data. Ecol. Appl. 19, 181–197. https://doi.org/10.1890/07-2153.1

R Core Team, 2020. R: A language and environment for statistical computing. R foundation for statistical computing, Vienna, Austria. Available at: https://www. R-project.org/.

Ripple, W.J., Beschta, R.L., 2012. Trophic cascades in Yellowstone: The first 15 years after wolf reintroduction. Biol. Conserv. 145, 205–213. https://doi.org/10.1016/j.biocon.2011.11.005

Sing, T., Sander, O., Beerenwinkel, N., Lengauer, T., 2005. ROCR: visualizing classifier performance in R. Bioinformatics, 21, 3940–3941.

Smith, J.B., Nielsen, C.K., Hellgren, E.C., 2016. Suitable habitat for recolonizing large carnivores in the midwestern USA. Oryx, 50, 555–564. https://doi.org/10.1017/S0030605314001227

Stauffer, G., Roberts, N.M., MacFarland, D., van Deelen, T.R., 2020. Evaluation of alternative methods for estimating wolf abundance in Wisconsin, USA. Wisconsin Department of Natural Resources, Wisconsin.

Stricker, H.K., Gehring, T.M., Donner, D., Petroelje, T., 2019. Multi-scale habitat selection model assessing potential gray wolf den habitat and dispersal corridors in Michigan, USA. Ecol. Modell. 397, 84–94. <https://doi.org/10.1016/j.ecolmodel.2018.12.021>

Svenning, J.-C., Skov, F., 2004. Limited filling of the potential range in European tree species. Ecol. Lett. 7, 565–573. https://doi.org/10.1111/j.1461-0248.2004.00614.x

Thiel, R.P., 1985. Relationship between road densities and wolf habitat suitability in Wisconsin. Am. Midl. Nat. 113, 404. <https://doi.org/10.2307/2425590>

Thomas, C.D., Cameron, A., Green, R.E., Bakkenes, M., Beaumont, L.J., Collingham, Y.C, ..., Williams, S.E., 2004. Extinction risk from climate change. Nature 427, 145–148. <https://doi.org/10.1038/nature02121>

Thuiller, W., Lafourcade, B., Engler, R., Araújo, M.B., 2009. BIOMOD - a platform for ensemble forecasting of species distributions. Ecography 32, 369–373. https://doi.org/10.1111/j.1600-0587.2008.05742.x

United States Census Bureau, 2010. Decennial census of population and housing. Available at: <https://www.census.gov/programs-surveys/decennial-census/decade/decennial-publications.2010.html>

United States Census Bureau, 2020. TIGER/Line shapefiles 2020: roads. Available at: <https://www.census.gov/geographies/mapping-files/time-series/geo/tiger-line-file.html>

United States Geological Survey, 1996. USGS EROS archive: digital elevation global 30 arc-second elevation (GTOPO30). https:/[/doi.org/10.5066/F7DF6PQS](https://doi.org/10.5066/F7DF6PQS)

United States Geological Survey, 2016. National hydrography dataset. Available at: https://www.usgs.gov/core-science-systems/ngp/national-hydrography/access-national-hydrography-products

USFWS (U.S. Fish and Wildlife Service), 2020. Gray wolf biological report: information on the species in the lower 48 United States. US Government Printing Office, Washington, DC.

Václavík, T., Meentemeyer, R.K., 2012. Equilibrium or not? modelling potential distribution of invasive species in different stages of invasion. Divers. Distrib. 18, 73–83. https://doi.org/10.1111/j.1472-4642.2011.00854.x

van den Bosch, M., Beyer Jr, D.E., Erb, J.D., Gantchoff, M.G., Kellner, K.F., MacFarland, D. M., Norton, D.C., ..., Belant, J.L., 2022. Identifying potential gray wolf habitat and connectivity in the eastern USA. Biol. Conserv. 273, 109708. <https://doi.org/10.1016/j.biocon.2022.109708>

Wheeldon, T., Patterson, B., Beyer, D., 2012. Coyotes in wolves' clothing. Am. Midl. Nat. 167, 416–420. <https://doi.org/10.1674/0003-0031-167.2.416>

Wolf, C., Ripple, W.J., 2016. Prey depletion as a threat to the world's large carnivores. R. Soc. Open Sci., 3, 160252. <https://doi.org/10.1098/rsos.160252>

Wolf, C., Ripple, W.J., 2017. Range contractions of the world's large carnivores. R. Soc. Open Sci., 4, 170052. <https://doi.org/10.1098/rsos.170052>

Wydeven, A.P., Wiedenhoeft, J.E., Schultz, R.N., Thiel, R.P., Jurewicz, R.L., Kohn, B.E., Van Deelen, T.R., 2009. History, population growth, and management of wolves in Wisconsin. In: Wydeven, A.P., Van Deelen, T.R., Heske, E. (Eds.), Recovery of Gray wolves in the Great Lakes region of the United States. Springer, New York, pp, 87–105. https://doi.org/10.1007/978-0-387-85952-1\_6

Yang, L., Jin, S., Danielson, P., Homer, C., Gass, L., Bender, S.M., ..., Xian, G., 2018. A new generation of the United States national land cover database: requirements, research priorities, design, and implementation strategies. ISPRS J. Photogramm. Remote Sens. 146, 108–123. https://doi.org/10.1016/j.isprsjprs.2018.09.006

## **CRediT authorship contribution statement**

**M. van den Bosch:** Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Visualization, Writing – original draft, Writing – review & editing. **D.E. Beyer:** Data curation, Funding acquisition, Writing – review & editing. **J.D. Erb:** Data curation, Funding acquisition, Writing – review & editing. **M.G. Gantchoff:** Data curation, Methodology, Writing – review & editing. **K.F. Kellner:** Data curation, Methodology, Writing – review & editing. **D.M. MacFarland:** Data curation, Funding acquisition, Writing – review & editing. **B.R. Patterson:** Methodology, Writing – review & editing. **J.L. Price Tack:** Data curation, Funding acquisition, Writing – review & editing. **B.J. Roell:** Data curation, Funding acquisition, Writing – review & editing. **J.L. Belant:** Conceptualization, Data curation, Funding acquisition, Methodology, Project administration, Resources, Supervision, Writing – review & editing.