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Regional analysis estimates extensive habitat impairment for the widespread, but vulnerable eastern box turtle

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ABSTRACT

Turtle populations are declining globally, yet limited attention has been directed toward understanding the conservation status of species perceived to be widespread and common. The goal of this study was to contribute to the understanding of the conservation status of the eastern box turtle (*Terrapene carolina*), a wide-ranging terrestrial generalist, in the northeastern United States (Maine to Virginia) by (1) characterizing relationships between occurrence and anthropogenic land use and (2) estimating the extent of land-use driven habitat impairment for the region. We used a regional dataset of occurrence records combined with pseudo-absences to develop species distribution models to first estimate the potential distribution in the northeastern United States and then predict habitat suitability within that distribution. We observed a strong positive relationship between probability of occurrence and canopy cover (within 180 m) and a strong negative relationship with hay/pasture fields (360 m), cultivated crops (180 m), impervious surface (360 m), and forest loss (since 2000; 1440 m). We estimate that approximately 51% of eastern box turtle habitat in the northeastern United States may be impaired by land use, with the majority of impairment predicted from Pennsylvania and Delaware south to Virginia. This study, in combination with previous long-term studies documenting population declines, suggests that greater attention to the conservation status of the eastern box turtle is warranted.

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1. Introduction

Turtle populations are declining worldwide and currently represent one of the most imperiled vertebrate clades (Lovich et al., 2018). The life history of most turtles — characterized by delayed sexual maturity, low juvenile survival, and low reproductive output — means that populations are susceptible to rapid decline from small increases in adult mortality (Congdon et al., 1993). Thus, most turtles are considered to be highly sensitive to anthropogenic activity that elevates the vulnerability of adults (Stanford et al., 2020). While most conservation attention has been directed toward the most vulnerable species, little is understood about the status of species perceived to be common, in part because they are generally a lower priority for distributional and population-level data collection (Dodd and Franz, 1993). However, if salient threats are not identified and addressed, there is the potential for common species to become threatened (Dodd and Franz, 1993, Kiester and Willey, 2015). Therefore, there is a clear need to understand the conservation status of common species, particularly for turtles.

The eastern box turtle (*Terrapene carolina*), a terrestrial generalist associated with both closed-canopy forest and early-successional communities (Nazdrowicz et al., 2008; Willey, 2010; Fredericksen, 2014; Rhodin et al., 2021), represents one of the most widely distributed turtle species in North America. Many factors are thought to negatively affect eastern box turtles, including habitat loss and degradation, illegal collection, road traffic, agricultural machinery, disease, fire, and climate change (Erb and Roberts, 2023), although little is known about the extent and nature of their effect on populations. While the eastern box turtle is currently considered to be globally "Secure" (NatureServe 2022), it is also listed as "Vulnerable" by the International Union for Conservation of Nature (van Dijk, 2011) and there is evidence that populations have declined dramatically throughout the species' range (Hall etal., 1999, Williams, 1961, Williams and Parker, 1987, Nazdrowicz et al., 2008, Jones et al., 2021), including a large population documented to be increasing (Dodd et al., 2012) until a recent catastrophic (>95%) decline (Jones et al., 2021). Such evidence of widespread decline suggests that threats to the species are pervasive, yet there is relatively limited understanding of which factors are driving declines and how they have affected habitat suitability across the species distribution.

With this study, we collected occurrence records from across the northeastern United States (within the *T. c. carolina* subspecies distribution) with the goals of (1) characterizing general relationships between occurrence and anthropogenic land use and (2) estimating the extent of land-use driven habitat impairment for the region. We expected that, as suggested in previous literature, the eastern box turtle would be negatively associated with agricultural cover (Erb and Jones, 2011) and development (Roe et al., 2021, Graham et al., 2022), and the combined effect of these variables would predict extensive habitat impairment throughout the region.

2. Study area

This study focused on the northeastern United States from Maine to Virginia, which encompasses the northeastern portion of the eastern box turtle's geographic distribution. This study was a part of a larger effort to develop a status assessment and conservation plan for the eastern box turtle in this region. We do not include spatially-explicit population location information due to the vulnerability of turtles, and eastern box turtles in particular, to poaching (Sung and Fong, 2018).

3. Methods

3.1. Occurrence records

We collected eastern box turtle occurrence records from state agencies, natural heritage programs, reptile atlas projects, and personal datasets of the authors. In cases where descriptive location information was available, we compared coordinates to location descriptions to confirm accuracy and removed records that were inaccurate. We excluded all records with accuracy >200 m. We also excluded records from Maine because the widely scattered points are believed to mostly represent escaped pets rather than natural occurrences (Derek Yorks, ME IFW, pers. comm.). We excluded records >30 years prior to the start of this study (i.e., before 1990) from consideration in analyses, following similar landscape-level analyses of recent land use and habitat impairment (Willey et al., 2022). To reduce sampling bias, we randomly selected remaining records that maintained a minimum of two km separation distance.

3.2. Pseudo-absences

We did not have consistent information about where eastern box turtles do not occur (i.e., "true" absences) and thus relied upon randomly generated locations, hereafter referred to as "pseudo-absences" (Chefaoui and Lobo, 2008, Barbet-Massin et al., 2012). Through visual inspection, it was clear that the occurrence dataset was spatially-biased toward roads (records are often reported by drivers who find turtles crossing roads). Therefore, we generated random points that were similarly biased toward roads using the "Create Spatially Balanced Points" tool in ArcMap 10.5 (Environmental Systems Research Institute, Inc., Redlands, CA). We generated approximately 10 pseudo-absences for every occurrence record (Barbet-Massin et al., 2012, Guisan et al., 2017) within three different subregions corresponding to New England states (Connecticut, Rhode Island, Massachusetts, Vermont, New Hampshire, and Maine), Mid-Atlantic states (New York, New Jersey, and Pennsylvania), and South states (Maryland, Delaware, District of Columbia, West Virginia, and Virginia). We use this subregional approach because we wanted pseudo-absences to reflect intraregional variation in both landscape context (e.g., road density) and sampling intensity (there tended to be a higher density of records in states where the species is considered more threatened and therefore tracked more extensively). We generated pseudo-absences within 100 km of occurrence records with the intention of capturing relevant climatic gradients determining the northern extent of the range.

3.3. Environmental variables

For each occurrence location and pseudo-absence location, we estimated the value of six climatic variables: minimum January temperature, mean July temperature, mean July precipitation, mean April precipitation, mean annual precipitation, and growing season degree days (GDD). The temperature and precipitation data represent 30-year normals (1981–2010; 800 m resolution rasters) acquired from the PRISM Climate Group (PRISM Climate Group 2021). We acquired growing season degree days, which represents the sum of daily mean temperatures above 10°C, from Designing Sustainable Landscapes (Plunkett et al., 2022). We also acquired elevation information from the National Elevation Dataset (Gesch, 2009).

Land use variables included percent canopy cover, proportion cultivated crops, proportion hay/pasture fields, mean imperviousness, proportion developed, road density, and proportion forest loss. We acquired all land use data, except forest loss, from the Multi-Resolution Land Characteristics Consortium 2016 National Land Cover Database (NLCD; Coulston et al., 2012, Yang et al., 2018). We acquired forest loss data from the Global Forest Change dataset (Hansen et al., 2013). This dataset (30-m resolution) estimates forest loss for each year since 2000, where forest loss is defined as a change in state from forest (vegetation >5 m) to a non-forest state. We resampled each variable to a 90-m resolution for computational purposes and measured each variable at six arbitrarily chosen spatial scales: the individual cell, 90 m, 180 m, 360 m, 720 m, and 1440 m. To place these scales in context of eastern box turtle movement, an average home range in the Northeast is approximately 4.5 ha (although variation in movement is highly variable among individuals; Erb and Roberts, 2023), which is equivalent to a 120 m radius circle. We extracted all raster values from presence/pseudo-absence locations using the "raster" package (Hijmans, 2019) in R statistical software (R Core Team 2022). We were interested in the extent to which the forest loss variable possibly represented timber harvesting, which, in contrast to urbanization and agricultural conversion, allow subsequent succession of natural communities to occur and do not further fragment the existing habitat. To address this question, we estimated the proportion of areas that experienced forest loss that were developed, cultivated crops, hay/pasture, or barren land (as defined by NLCD) using ArcMap.

3.4. Statistical analyses

We followed a two-stage process for estimating regional habitat impairment. First, we estimated the "potential" distribution by modeling the eastern box turtle climate niche in the study area and removing all open water habitats (as defined by NLCD). While this is a liberal approach, the generalist nature of the eastern box turtle within terrestrial communities suggests that they were likely primarily limited by wetlands and climate (Bleakney, 1958, Adler, 1968) prior to European colonization, although relatively little is known about how Native American populations influenced the distribution (Adler, 1970). We chose to not exclude woody emergent wetlands from the predicted potential distribution because, while many of these wetlands are clearly not suitable, populations can at least seasonally occupy portions of woody and emergent wetlands that either dry out or are very shallow (Donaldson et al., 2005).

We used logistic regression to relate presence and pseudo-absence locations to climate. First, three simple models were run for each variable that included either a linear term, a quadratic term, or a linear interaction with elevation. The variable(s) that performed best with respect to Akaike's Information Criterion (AIC; Burnham and Anderson, 2002) were selected for inclusion in the comparison of more complex models. While the driving ecological mechanism remains unclear, we considered an interaction between climate variables and elevation because the maximum suitable elevation threshold appears to vary throughout the range, perhaps in relation to climate. Previous distribution modeling efforts (e.g., DeLuca, 2015) have not considered elevation and presumably as a result, predicted substantial amounts of suitable habitat at high elevations where they do not occur. We examined correlations among variables and when correlations were high ($r > 0.7$), we kept the variables that performed best with respect to AIC. Next, models with all variable subsets were compared (where both variables in interactions had to be considered together) using the "MuMIN" package in R (Barton, 2016). We then used the top model to predict the potential distribution throughout the region using the "dismo" package (Hijmans et al., 2011) in R. To ensure a liberal estimate of potential distribution that emphasizes known occurrence locations, we chose a binary threshold for suitability that achieved sensitivity (true positive prediction rate) = 0.99. We assessed predictive ability by performing a five-fold cross-validation procedure (Guisan et al., 2017). To avoid over-predicting the potential distribution at the northern edge of the range, we only considered areas within 50 km of a known record.

Next, we modeled habitat impairment via land use using only records and pseudo-absences that fell within the predicted potential distribution. Similar to modeling climate, we used logistic regression to compare (using AIC) three simple models for each land cover-scale combination that included either a linear term, quadratic term, or a linear interaction with GDD. We examined an interaction with GDD because, like most ectotherms, eastern box turtle life history is strongly influenced by climate, and we expected that increased growth rates and (possibly) reproductive output in warmer areas could mediate population relationships with land cover. We chose the best performing scale and term(s) for each land cover type and, after removing highly correlated variables, compared all variable subsets to find a "top" model that included multiple land cover types. Last, we performed a five-fold cross-validation procedure and then predicted suitability throughout the potential distribution. We selected a suitability threshold by taking the value that maximized the combined true positive and true negative rates (Liu et al., 2005, Hallfors et al., 2016). We assessed model performance using the Area Under the Curve metric (Guisan et al., 2017).

We provided further context for areas predicted to be suitable within the potential distribution by summarizing the percent of suitable habitat that is characterized as developed (Yang et al., 2018) or woody or emergent wetland (Yang et al., 2018). We summarized habitat impairment and these metrics by state and United States Environmental Protection Agency (EPA) Level 3 Ecoregion. EPA Ecoregions are intended to represent ecosystems and environmental resources that are generally similar (Omernik, 1987).

4. Results

Our occurrence database included 15,858 records, spanning 12 states including Maine (17), New Hampshire (122), Massachusetts (4030), Rhode Island (71), Connecticut (735), New York (403), New Jersey (715), Pennsylvania (3153), Maryland (633), Delaware (258), District of Columbia (23), West Virginia (1362), and Virginia (4336). The occurrence dataset was reduced to 3990 records after data cleaning described in section 3.1 and applying the 2-km minimum separation distance. The top performing model for potential distribution included interactions between elevation and both minimum January temperature and annual precipitation (Table 1). Cross-validation yielded mean AUC = 0.63 (range 0.62–0.64). The full potential distribution model (i.e., using all data) predicted 299,210 km^2 of habitat across the study area (Table 2, Fig. 1).

Simple land cover models indicated strong positive relationships between probability of eastern box turtle occurrence and percent canopy cover (180 m, influenced by GDD), and strong negative relationships with cultivated crops (180 m, quadratic), hay/pasture (360 m, influenced by GDD), imperviousness (360 m, quadratic), development (360 m, quadratic), road density (360 m, quadratic), and forest loss (1440 m, linear; Fig. 2).

Our assessment of the forest loss variable revealed that development, cultivated crops, hay/pasture, or barren land corresponded to only 11% of the area that experienced forest loss. Imperviousness, development, and road density were highly correlated ($r > 0.7$) and thus only imperviousness, which performed best with respect to AIC, was considered in more complex models. The top land cover model included cultivated crops, an interaction between hay/pasture and growing degree days, imperviousness, and forest loss, but not canopy cover (Table 1). Cross-validation yielded mean AUC = 0.66 (range 0.65–0.67). The full model (i.e., using all data) predicted that 51% of the potential distribution is currently impaired (Fig. 1A). Within suitable habitat, 11% (5% of potential distribution) was classified as woody/emergent wetlands and 10% (5% of potential distribution) was classified as some form of development. Our assessment showed substantial variation in the extent of impairment among states (Table 2, Fig. 3) and ecoregions (Appendix A).

5. Discussion

Our findings suggest that the eastern box turtle has experienced extensive habitat impairment in the northeastern United States, with approximately 51% of the predicted potential distribution possibly impaired by anthropogenic land use. This estimate is comparable to estimates of habitat loss or impairment for other turtle species considered more threatened in the region, such as the wood turtle (*Glyptemys insculpta*; 58%, Willey et al., 2022). To the extent that survival and reproduction are negatively affected by habitat impairment, and when considered with the body of literature demonstrating individual population declines throughout the range (Hall et al., 1999, Williams and Parker, 1987, Nazdrowicz et al., 2008, Jones et al., 2021), this study supports the contention that this species has likely experienced widespread population declines (Dodd, 2001, Roe et al., 2021).

These results indicate that the highest proportional levels of habitat impairment have occurred in Virginia (64%), Delaware (60%), Pennsylvania (58%), and the District of Columbia (84%, although District of Columbia represents <0.001% of potential habitat). When low-intensity development (e.g., roads) and woody/emergent wetlands (many of which are likely not suitable for eastern box turtles) were taken into account, Delaware (13%), New Jersey (27%), Maryland (29%) had the lowest levels of unimpaired upland, apart from District of Columbia (7%). West Virginia appears to represent a stronghold for the species in the Northeast, with not only the lowest proportional impairment and highest area of suitable habitat (regardless of whether additional low-intensity development and wetland habitat are taken into account), but also some of the least fragmented landscapes (likely due to the mountainous terrain; Fig. 2A). There also appear to be substantial disparities in impairment among ecological contexts, with ecoregions at the core of the regional distribution, such as the Piedmont and Southeastern Coastal Plains, experiencing apparently severe habitat impairment (83% and 60% respectively), and others such as the Central Appalachians experiencing relatively low impairment (24%). Notably, when excluding wetlands and low-intensity development, the Middle Atlantic Coastal Plain and Atlantic Coastal Pine Barren ecoregions displayed extensive declines in unimpaired habitat, with only 15% and 28% of the potential distribution remaining, suggesting that these ecoregions might be more vulnerable than our basic predictions indicate.

The observed negative associations with urbanization and agriculture lend support to the notion that these land uses are driving eastern box turtle population declines. Urban environments may lead to lower adult and juvenile survival through factors such road mortality, incidental collection, and human-subsidized predation (Gibbs and Shriver, 2002, Garber and Burger, 1995, Marchand and Litvaitis, 2004). While there is limited research on the subject, a few studies have documented negative relationships between density and urbanization (Roe et al., 2021, Graham et al., 2022). Frequently mowed hay fields may represent a particularly salient threat

Table 1
Coefficients (standard error) for the potential distribution and habitat impairment models for eastern box turtle in the northeastern United States. Squared terms indicate quadratic relationships. Interaction coefficients are represented by hyphenated covariates. Asterisks indicate coefficients for 95% confidence intervals that do not overlap zero. All covariates were scaled for the models in this table such that mean = zero and standard deviation = one. MJT = minimum January temperature; AP = annual precipitation; GDD = growing degree days.

Model	MJT	AP	Elevation	MJT-Elevation	AP-Elevation
Potential Distribution	0.49* (0.02)	0.15* (0.02)	–0.34* (0.02)	0.36* (0.03)	–0.1* (0.02)

Model	$Crops^2$ 180 m	Hay^2 360 m	GDD	$Impervious^2$ 360 m	Forest Loss 1440 m	Hay-GDD
Habitat Impairment	–0.11* (0.009)	–0.44* (0.024)	0.12* (0.02)	–0.37* (0.02)	–0.36* (0.03)	0.12 (0.03)

Table 2
Summary, by state, of predicted eastern box turtle habitat impairment in the northeastern United States as well as the percent of unimpaired habitat categorized by the National Land Cover Database as wetland or developed.

State	Area (km^2)	Area impaired (km^2)	% impaired	Within unimpaired habitat	
				% wetland	% developed
District of Columbia (DC)	160	134	84	6	48
Virginia (VA)	97,107	61,983	64	9	7
Delaware (DE)	5000	2989	60	51	16
Pennsylvania (PA)	56,451	32,564	58	2	11
Maine (ME)	983	559	57	25	8
New Hampshire (NH)	4787	2564	54	17	11
Maryland (MD)	23,266	11,988	52	26	14
Vermont (VT)	207	105	51	3	9
New York (NY)	16,131	7987	50	1	16
New Jersey (NJ)	18,823	8238	44	34	17
Massachusetts (MA)	14,627	6163	42	20	16
Rhode Island (RI)	2693	1032	38	17	14
Connecticut (CT)	11,462	3348	29	11	14
West Virginia (WV)	47,514	11,807	25	0	5
All states	299,210	151,462	51	11	10

because turtles are often drawn to fields (Erb and Jones, 2011) from adjacent forest for increased solar exposure (for basking and/or nesting) and foraging opportunities. Although studies have suggested mortality associated with hay fields may negatively affect populations (Nazdrowicz et al., 2008, Erb and Jones, 2011), we are unaware of any demonstrating negative relationships with agriculture across populations. Conversion of suitable habitat to cultivated crop cover results in the loss of habitat, but in contrast to hay fields, may not have the same negative effect on surrounding areas because crop fields are likely less attractive for thermoregulation and foraging — this may explain why the relationship with crops (180 m) was characterized by a smaller spatial scale compared to hay/pasture (360 m). Future research should consider examining the varying effects of agriculture on population demographics both within and across populations.

Although our measure of forest loss (Hansen et al., 2013) reflects a range of causes, our assessment indicated that development and agriculture made up a relatively small proportion (11%) of areas with forest loss. Within our study area, the highest proportions of forest loss within 1440 m occurred in Virginia where pine plantations can constitute most of the forest area in many locations and harvesting for wood pulp is widespread (Oswalt et al., 2019; Fig. 4), indicating that the high-intensity large-scale commercial tree cultivation, and associated management practices, that occurs in Virginia might be driving the negative association with forest loss (Fox et al., 2007). This is further supported by our finding that forest and shrub/herbaceous cover made up the majority of areas that had experienced forest loss, which is consistent with habitat conditions following forest harvest (Greenberg et al., 2011).

Although more research is needed, studies focused on small-scale forestry (e.g., patch cuts) have not reported eastern box turtle mortality related to management activities (e.g., Currylow et al., 2012), suggesting limited population-level effects of low-intensity canopy removal. However, we are unaware of any studies that have examined the effects of large-scale, high-intensity forestry practices that characterize the southeastern portion of our study region (e.g., the Virginia Piedmont; Fig. 4). Forestry in this region uses short rotations that increase the exposure of turtles to heavy machinery and may increase mortality (via crushing and soil compaction), regardless of whether turtles are active or overwintering underground. Forestry in this area also involves intensive site preparation to control competing hardwood vegetation, such as disking and prescribed burning, which are also likely to increase mortality (e.g., see Erb and Jones, 2011, Jones et al., 2021, Buchanan et al., 2021). Closed-canopy conditions serve as both overwintering habitat and thermal refugia during summer when temperatures can approach lethal levels (>41.5°C) in canopy openings (Hutchison et al., 1966, Currylow et al., 2012, Roe et al., 2017). Therefore, while high-volume canopy removal that eliminates entire patches of forest may create suitable early-successional habitat, the lack of remaining closed-canopy conditions may trigger a dispersal response (e.g., see Dodd et al., 2006) that could further increase mortality rates via exposure to hazards. Dispersal-associated mortality may be especially acute within highly fragmented landscapes such as those in southeastern Virginia (Fig. 4). The possible negative effects of high-intensity timber harvesting are of particular conservation concern for the eastern box turtle given that similar practices occur at even larger scales throughout much of the southern portion of the species distribution (Fig. 5; Masek et al., 2011, Hansen et al., 2013, Oswalt et al., 2019).

We want to emphasize that these results should not be interpreted as evidence that all practices that remove forest canopy — which vary widely in their purpose and environmental impact — are universally negative for eastern box turtles, and therefore should not be used to argue against forest management for wildlife. In fact, smaller-scale forest management practices (e.g., patch cutting) that employ longer rotations without intensive site preparation may even have positive effects for eastern box turtle populations in highly forested contexts by providing a gradient in microclimate, direct and diffuse solar radiation, forage availability (Griffiths and Christian, 1996), and protective cover (Greenberg, 2001, Agha et al., 2018), particularly if operations are carefully planned (ideally with spatial population data) and mortality is minimized using best management practices (e.g., Natural Heritage and Endangered Species Program, 2016, Erb and Roberts, 2023). Forest management also clearly benefits a host of other priority species dependent on shrubland habitats, including plants, invertebrates, birds, and mammals (Litvaitis, 2003, Roberts et al., 2017, Roberts and King, 2017, Milam

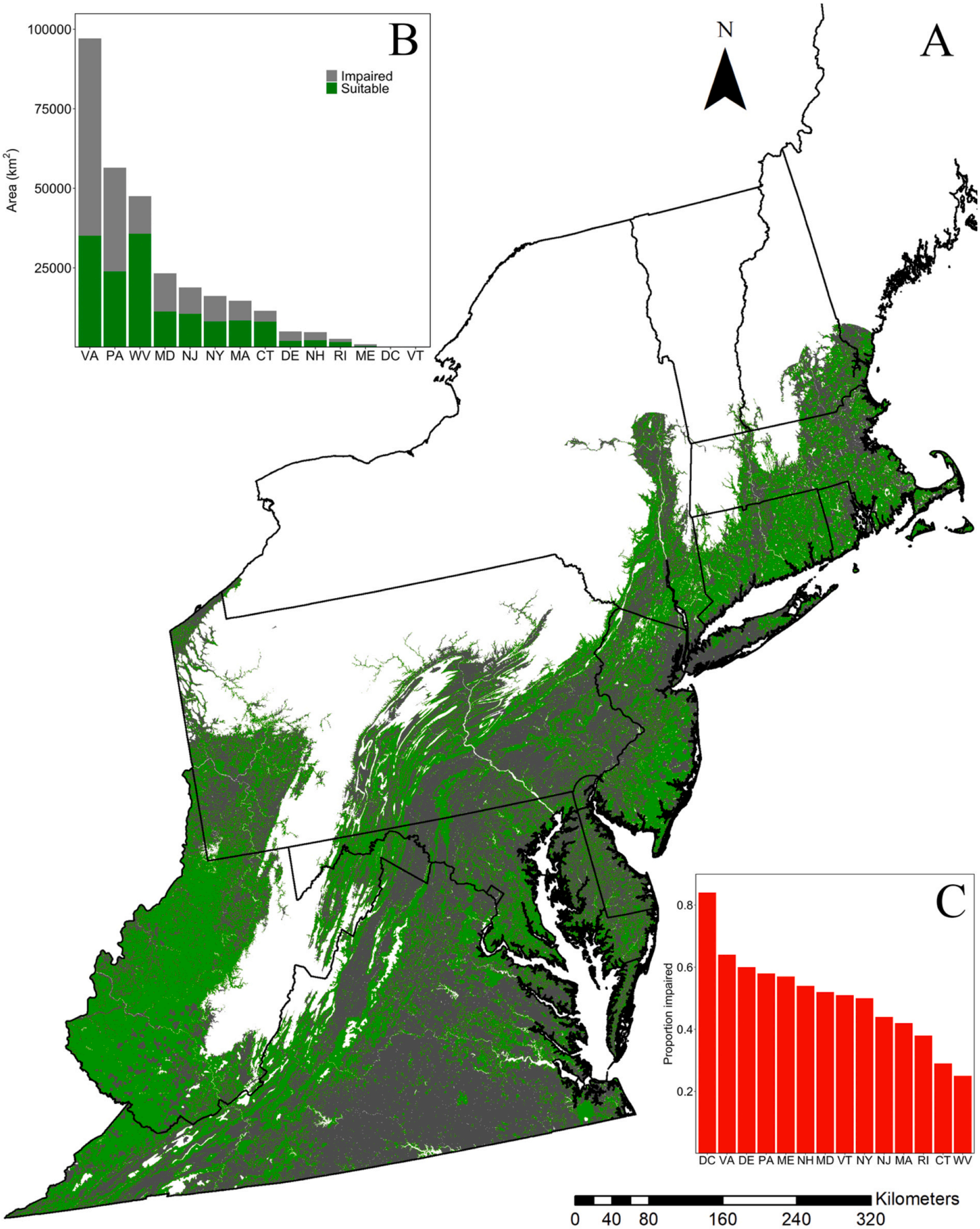

Fig. 1. Predicted eastern box turtle habitat impairment (green = suitable, gray = impaired, white = climatically unsuitable) within the northeastern U.S. (A) as well as area (B) and proportion (C) of impaired and suitable habitat within each state in the region. ME = Maine, NH = New Hampshire, VT = Vermont, MA= Massachusetts, RI = Rhode Island, CT = Connecticut, NY = New York, N*J* = New Jersey, PA = Pennsylvania, DE = Delaware, MD = Maryland, WV = West Virginia, VA = Virginia.

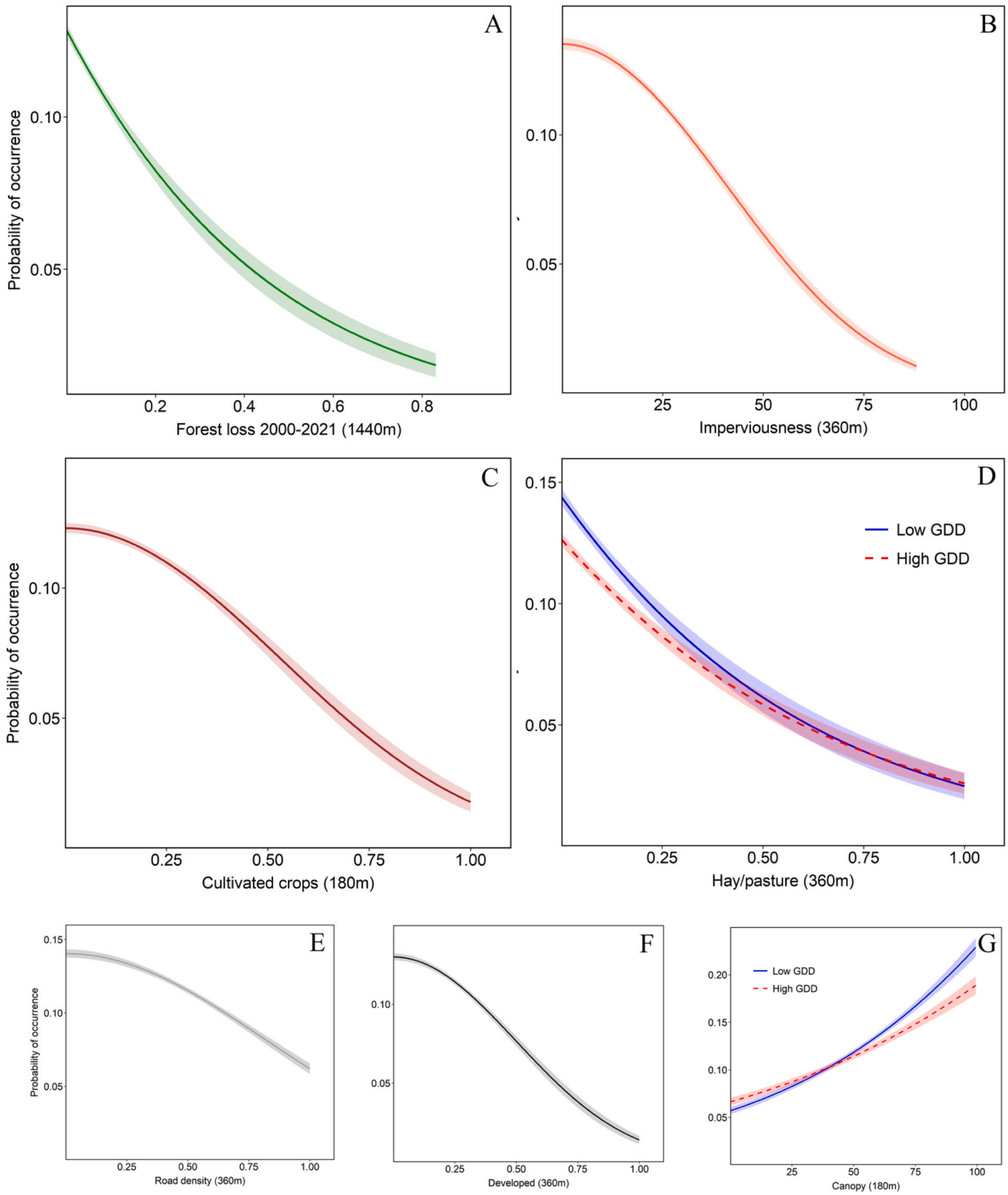

Fig. 2. Probability of occurrence of eastern box turtles in the northeastern U.S. in relation to proportion forest loss within 1440 m (A), percent imperviousness within 360 m (B), proportion cultivated crops within 180 m (C), proportion hay/pasture within 360 m (D), proportion road density within 360 m (E), proportion developed within 360 m (F), and percent canopy cover within 180 m (G). Plots depict predictions for simple models only containing a single variable or an interaction with growing season degree days (GDD). Developed land (E), road density (F), and canopy cover (G) were not included in the top model used to predict habitat impairment.

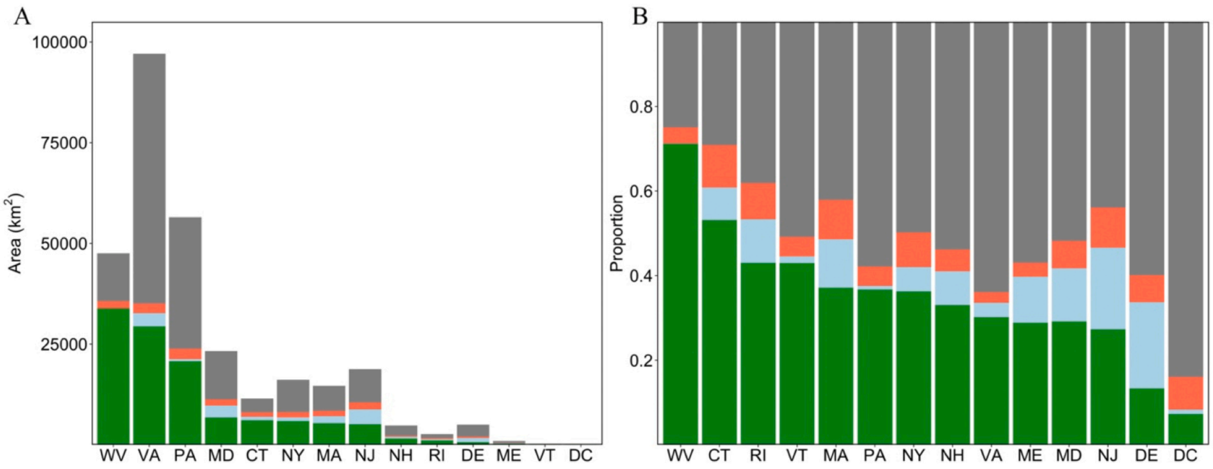

Fig. 3. Area (A) and proportion (B) of impaired habitat (gray/top portion of bars), suitable upland habitat (green/bottom portion of bars), developed areas within suitable habitat (red/second from top portion of bars), and woody/emergent wetlands within suitable habitat (blue/third from top portion of bars) within each state. ME = Maine, NH = New Hampshire, VT = Vermont, MA= Massachusetts, RI = Rhode Island, CT = Connecticut, NY = New York, NJ = New Jersey, PA = Pennsylvania, DE = Delaware, MD = Maryland, WV = West Virginia, VA = Virginia.

et al., 2022).

When considered within the context of historic land use, the potential negative relationship with high-intensity large-scale canopy removal suggests the regional population has potentially experienced even greater declines than our assessment indicates. By the mid 19th century much of the northeastern U.S. was completely deforested (Thompson et al., 2013) and therefore many local populations may have been extirpated, severely reduced in size, or isolated prior to reforestation during the 20th century. Despite widespread restoration of suitable conditions, the window of time since maximum deforestation (approximately 1850–present) may only represent 5–12 (or fewer) generations (e.g., see Miller (2001) and Cortés-Rodríguez et al. (2021) for generation length estimates for other *Terrapene* species) and thus many populations could still be recovering, even with minimal additional anthropogenic threats to adult, juvenile, and nest survival. Historical land-use patterns have been shown to shape contemporary herpetofaunal communities in other ecosystems. For example, legacy land use better predicts ornate box turtle (*T. ornata*) occurrence than current vegetation conditions in North American prairies (Royal et al., 2022). However, it is possible that past forest loss was less detrimental for populations than contemporary operations given that heavy machinery was not available.

Our findings indicate that land cover relationships may vary climatically, although the interactions that we observed between land cover and growing season degree days (GDD) were relatively minimal. It is possible our data (i.e., presence/pseudo-absences) was not sufficient for examining GDD-dependent land-use relationships, or a broader GDD gradient is needed. Since individual turtles can often occupy areas long after severe population decline and functional extinction, it is possible that other response variables that are more sensitive to land use, such as abundance, may display a stronger interactive relationship with GDD.

We recommend against using these results to draw conclusions about relatively small spatial extents (e.g., individual populations or subpopulations). We used a relatively large raster resolution (90 m), which means that these predictions are unable to reflect fine-scale conditions that might be important for populations. Misclassifications are also known to be present within the National Land Cover Database (Brown et al., 2016) and therefore we cannot ensure that all locations are without error. These analyses are also imperfect in that the use of true absence data instead of pseudo-absences could yield different relationships. For example, the random nature of pseudo-absence placement means that some were placed within suitable contexts, which could result in weaker predicted relationships with land use than true presence/absence data might produce. The longevity of the species also means that unsuitable contexts that still harbor turtles long after population decline, such as suburban areas and small forest fragments within highly developed areas, likely had inflated suitability predictions. The opportunistic nature of the data (i.e., we combined datasets and were unable to implement a standardized random data collection effort) also means that our database may harbor biases that could have influenced our results. While we attempted to account for some of these biases (e.g., road bias), it is possible others may be present. For example, although we had reason to suspect a negative relationship with agriculture, eastern box turtles in agricultural fields might be less likely to be found or reported to state agencies or other databases, thus resulting in a stronger negative relationship than actually occurs, and a potential overestimate of habitat impairment. Last, while eastern box turtles are forest-associated, populations are highly dependent upon open habitats for thermoregulation and nesting (particularly in colder portions of the distribution), and therefore, in contrast with our results, the deep interior of large forest blocks may not actually represent suitable habitat in some portions of the range. However, research is needed to confirm this hypothesis.

While the Area Under the Curve (AUC) metric values (0.65–0.67) for the impairment model are considered relatively "low" (Guisan et al., 2017), there were a couple of reasons why we expected that AUC may not be a perfect indicator of predictive ability for this species. First, because eastern box turtles are generalists and their habitat is relatively common across the Northeast, randomly generated pseudo-absences were fairly likely to be placed in eastern box turtle habitat. Therefore, in many cases the model may not

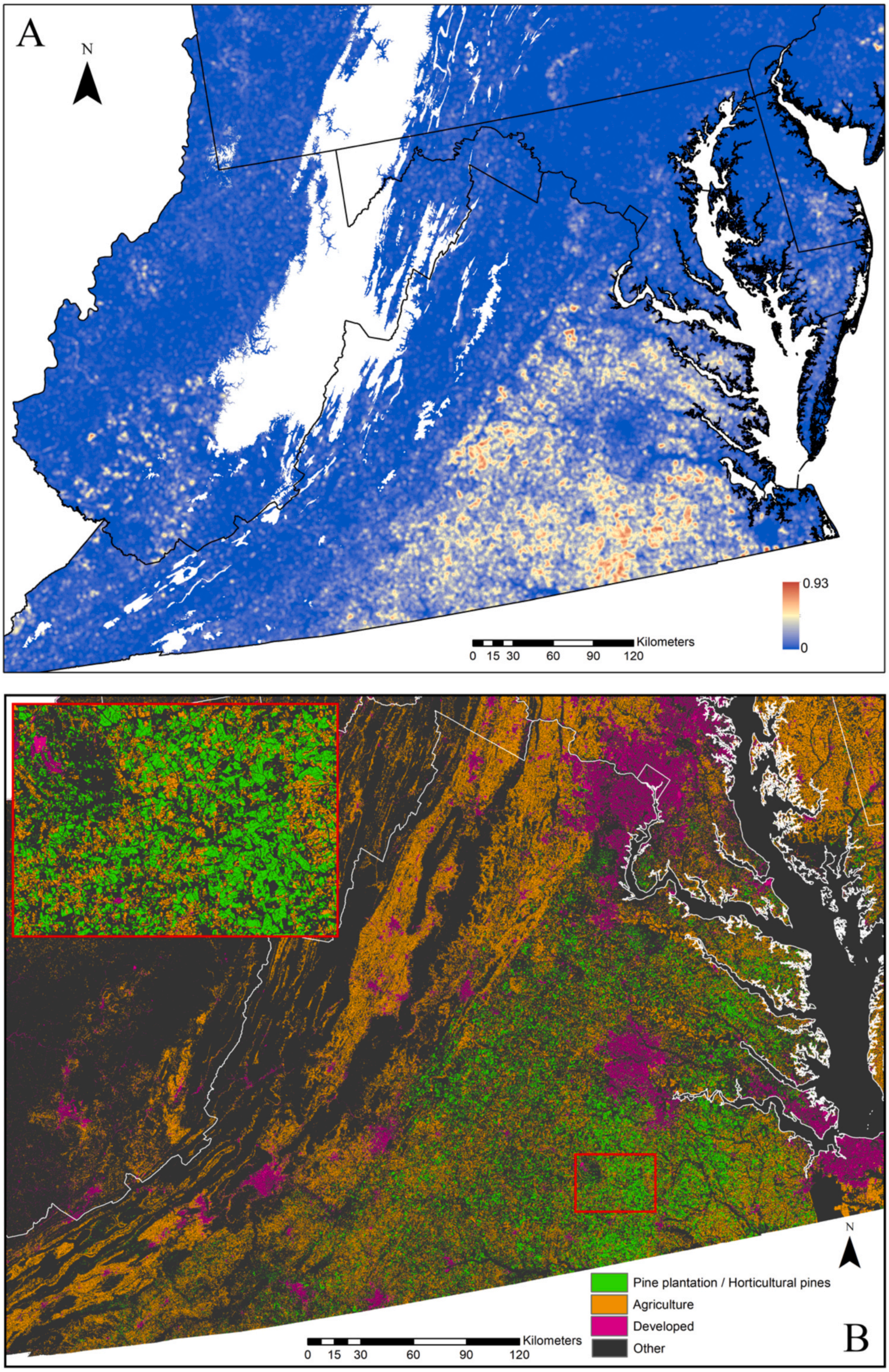

Fig. 4. Maps of the southern portion of the study area displaying the proportion forest loss from 2000–2021 within 1440 m (A) and as well as different cover types (B). White areas within state boundaries (black lines) in map A are locations considered outside of the potential eastern box turtle distribution. The land cover dataset in map B was accessed from Designing Sustainable Landscapes in 2017 (McGarigal et al. 2020).

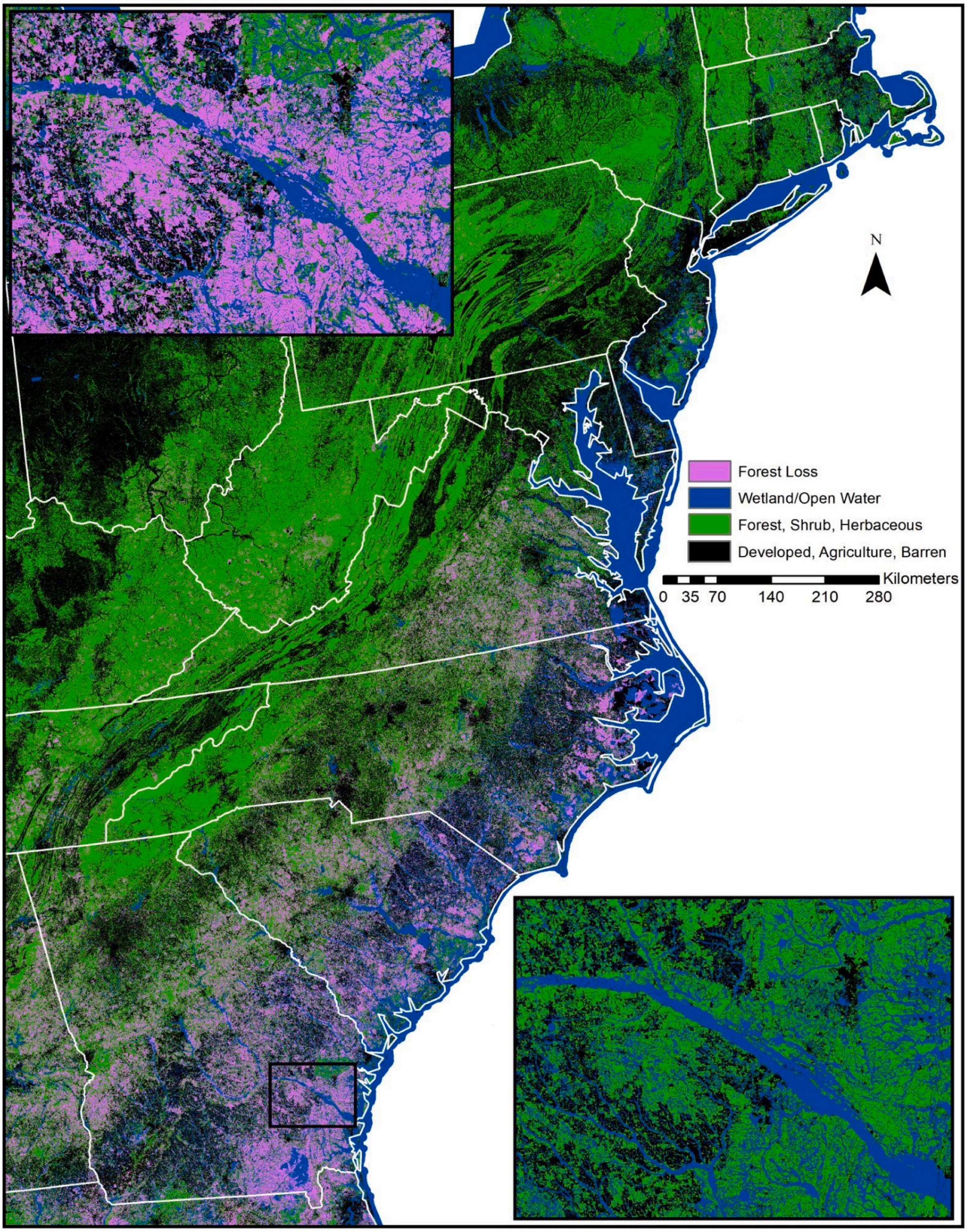

Fig. 5. Forest loss from 2000–2021 (purple; Hansen et al. 2013) in the southern portion of the eastern box turtle distribution. Both inset maps show the same area (indicated by black box at the bottom of the map). The top left inset shows the extent of areas that have experienced forest loss. The bottom right inset does not include forest loss data, illustrating how much of the landscape was not converted to development or agriculture and thus appears as potentially suitable habitat when not considering the extent and intensity of management (e.g., disking, fire, and other practices in addition to canopy removal with heavy machinery) that often occurs in such highly managed forest landscapes.

have been able to "accurately" predict a pseudo-absence location, thus decreasing the AUC value, but leading to a more ecologically accurate result (i.e., the area was accurately predicted to be suitable despite the presence of a pseudo-absence). Second, as previously mentioned, eastern box turtles display relatively extreme longevity and as a result, single (or relatively few) individuals may remain within an area despite severe habitat loss/degradation and functional extinction of the local population. Therefore, we expect that in some cases occurrence records actually represented unsuitable conditions and thus may have been harder for the model to predict, leading to additional reduction in AUC. Although we believe these AUC values undervalue the predictive ability of this model, it is nevertheless important to recognize that these results represent estimates with error.

6. Conclusion

This study suggests that habitat across a large proportion of the eastern box turtle range is impaired, and to the extent that survival and reproduction are negatively affected by habitat impairment, these findings support the contention (Dodd, 2001, Roe et al., 2021) that this species has potentially undergone widespread population declines. While the area of potentially suitable remaining habitat is greater than those of aquatic or semi-aquatic species that are considered more threatened (e.g., spotted turtle [*Clemmys guttata*], Blanding's turtle [*Emydoidea blandingii*], wood turtle), wetlands currently receive far greater protection under federal and state legislation in the United States than upland eastern box turtle habitat. Moreover, due to the perceived commonness of the species, there have been few standardized efforts to document populations and demographic trends (although see Roe et al., 2021) and thus, there is often very little understanding of whether populations even occur within seemingly suitable contexts, let alone their conservation status. We believe an important immediate next step is to begin to address data-deficiencies by establishing a collaborative effort to implement both rapid and long-term population monitoring efforts across not only the northeastern United States, but also the broader species distribution.

CRediT authorship contribution statement

Willey Lisabeth: Funding acquisition, Investigation, Writing – review & editing. **Erb Lori:** Conceptualization, Funding acquisition, Investigation, Project administration, Writing – original draft, Writing – review & editing. **Roberts H. Patrick:** Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Visualization, Writing – original draft, Writing – review & editing. **Kleopfer John:** Writing – review & editing. **Ravesi Michael:** Investigation, Writing – review & editing. **King David I.:** Investigation, Writing – review & editing. **Zarate Brian:** Investigation, Writing – review & editing. **Oxenrider Kevin:** Methodology, Writing – review & editing. **Nazdrowicz Nathan:** Investigation, Writing – review & editing. **Jones Michael T.:** Investigation, Methodology, Writing – review & editing. **Buchanan Scott:** Investigation, Writing – review & editing.

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 data that has been used is confidential.

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APPENDIX A. Table and figures associated with the summary of eastern box turtle habitat impairment within EPA Level 3 Ecoregions in the northeastern United States

Table A1
Summary, by Environmental Protection Agency Level 3 Ecoregion, of predicted habitat impairment within the predicted eastern box turtle

distribution in the northeastern United States. We also include percent of unimpaired habitat categorized as wetland or developed by the National Land Cover Database.

EPA Ecoregion Level 3	Area (km^2)	Area impaired (km^2)	% impaired	Within suitable habitat	
				% wetland	% developed
Atlantic Coastal Pine Barrens	13,869	5841	42	32	20
Blue Ridge	9555	3264	34	0	4
Central Appalachians	24,815	6040	24	0	5
Eastern Great Lakes Lowlands	784	519	66	20	15
Erie Drift Plain	2532	1542	61	17	9
Middle Atlantic Coastal Plain	22,542	11,892	53	57	12
North Central Appalachians	1063	159	15	3	12
Northeastern Coastal Zone	36,803	16,054	44	16	16
Northern Allegheny Plateau	990	164	17	9	8
Northern Appalachian and Atlantic Maritime Highlands	8733	2734	31	8	9
Northern Piedmont	30,882	21,398	69	6	20
Piedmont	33,170	27,478	83	4	9
Ridge and Valley	58,603	31,446	54	1	6
Southeastern Plains	19,511	11,658	60	18	13
Western Allegheny Plateau	34,992	11,255	32	0	7

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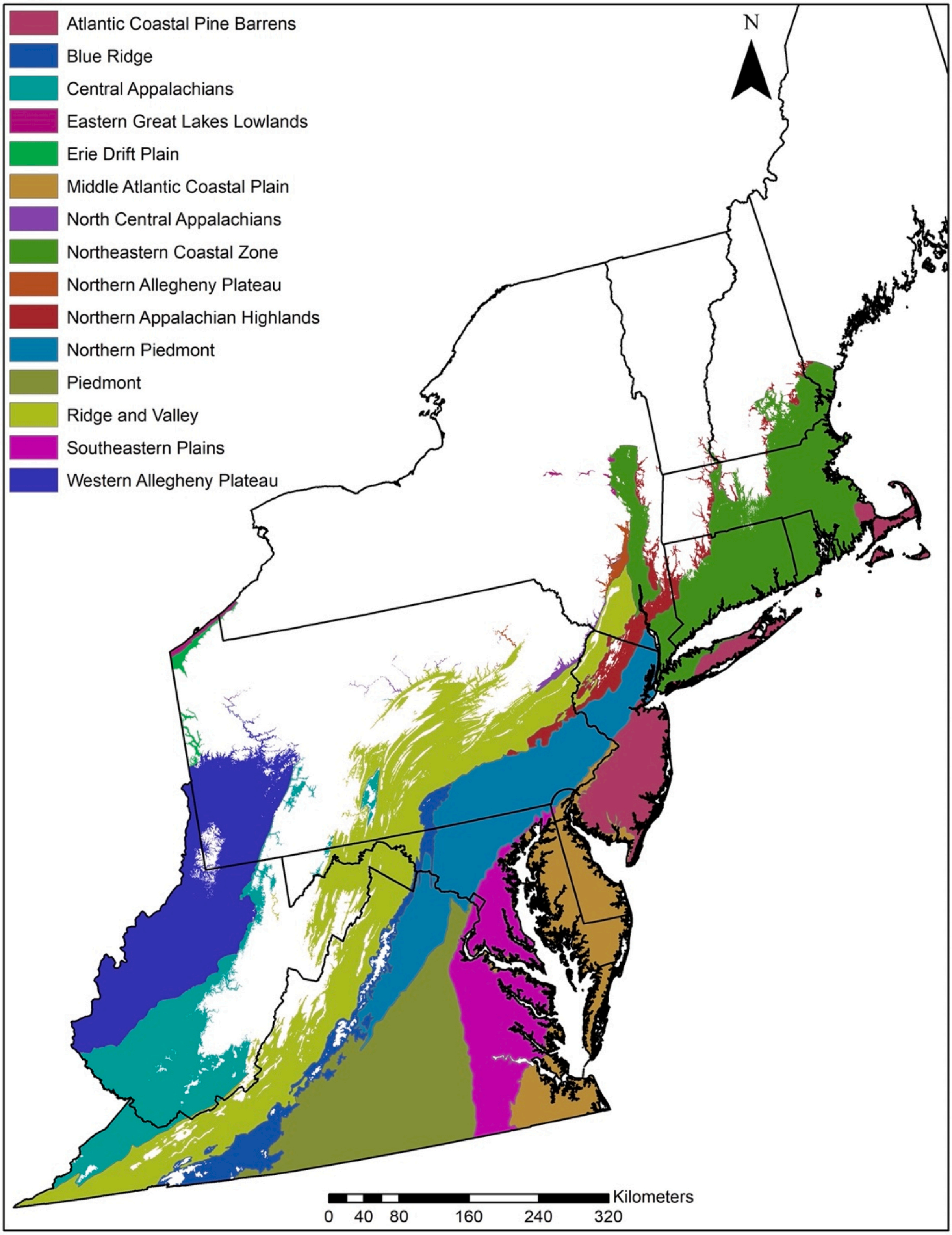

Figure A1. EPA Level 3 Ecoregions within the predicted eastern box turtle distribution in the northeastern United States.

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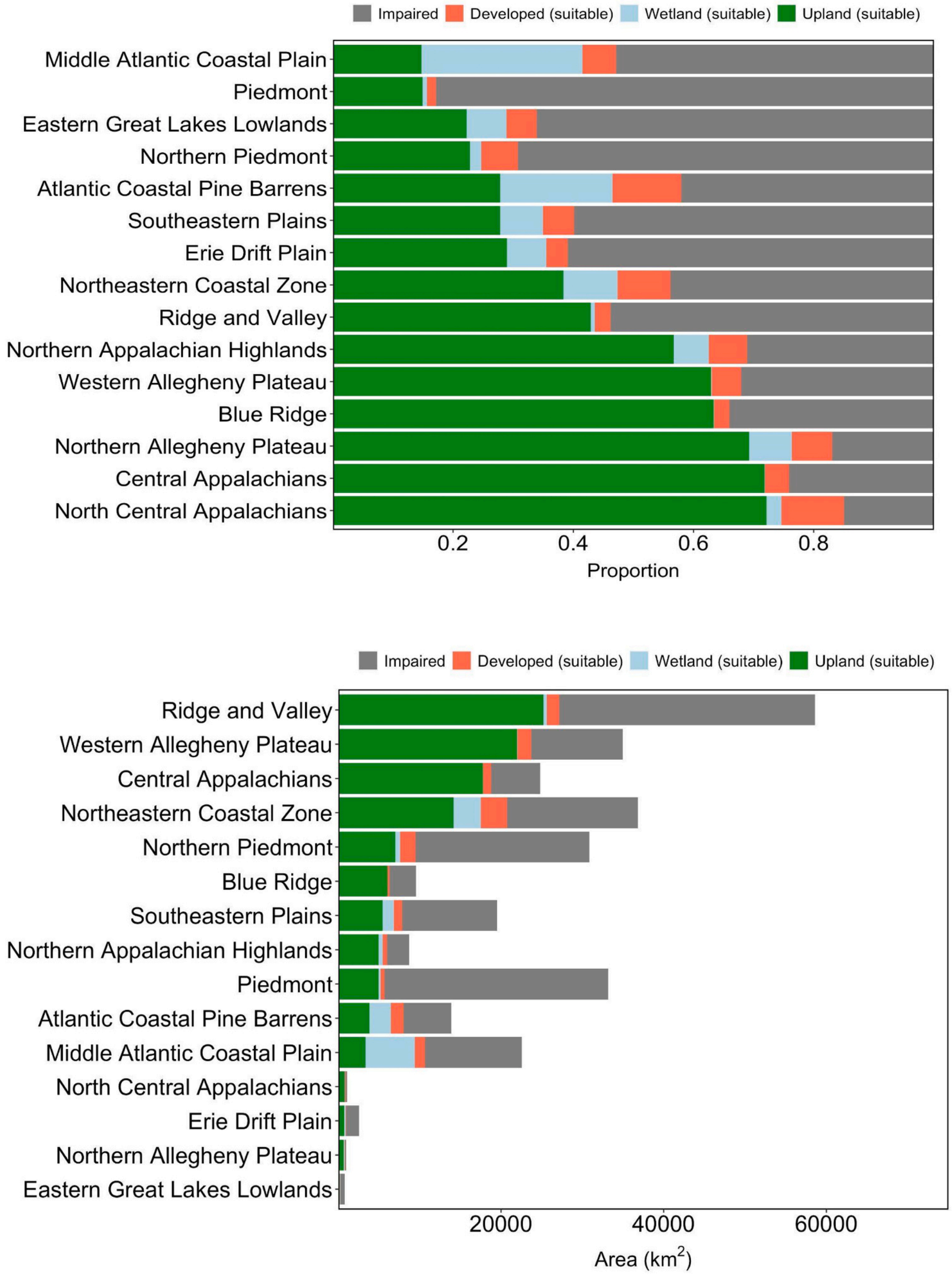

Figure A2. Proportion (top) and area (bottom) of impaired habitat, suitable upland habitat, developed areas (within suitable habitat), and woody/emergent wetlands (within suitable habitat) within Level 3 EPA Ecoregions within the eastern box turtle distribution in the northeastern United States.

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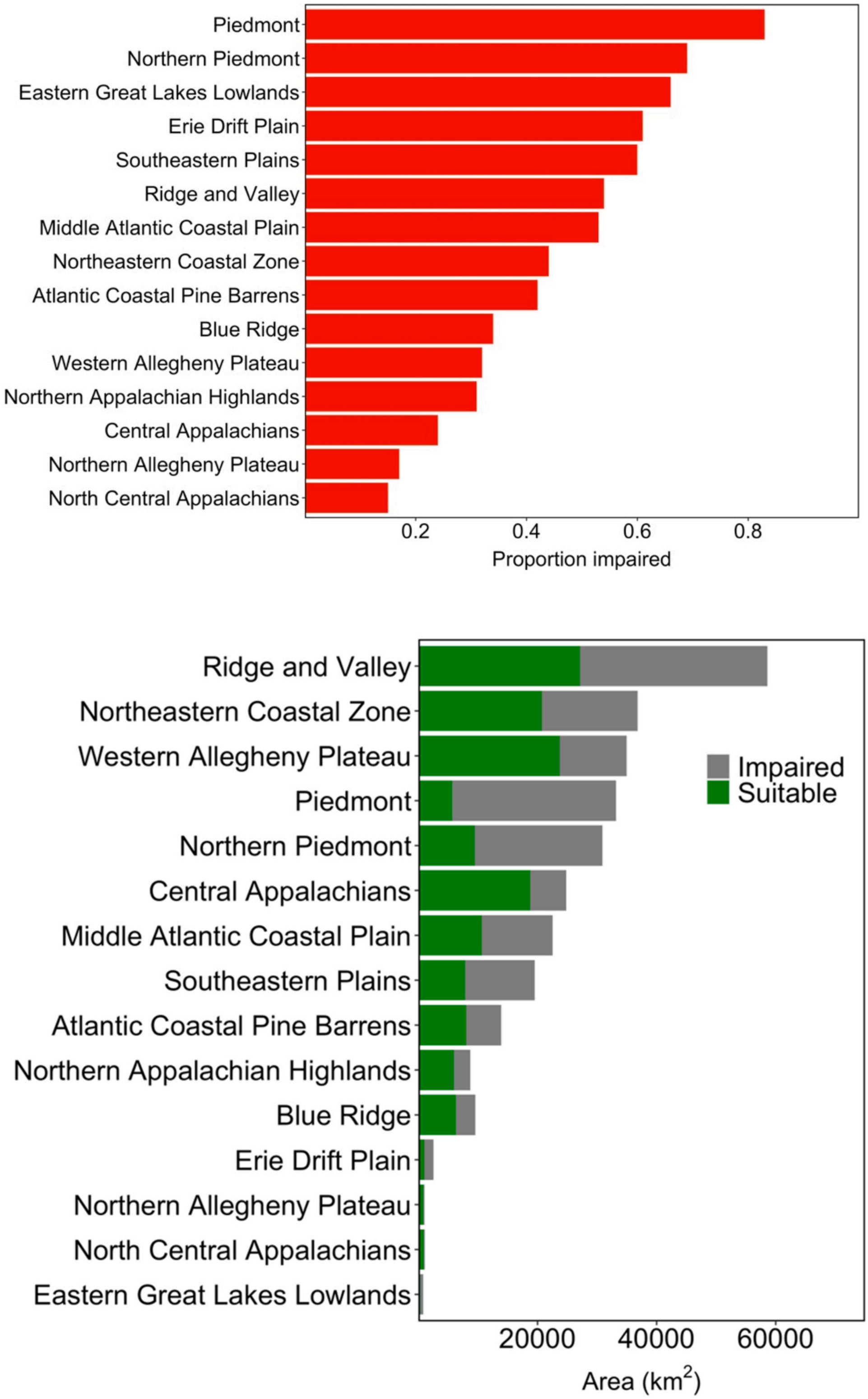

Figure A3. Proportion (top) and area (bottom) of habitat within EPA Level 3 Ecoregions within the predicted eastern box turtle distribution in the northeastern United States.

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