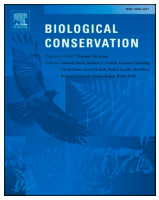
Biological Conservation 283 (2023) 110088

Contents lists available at ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon



Effects of landscape structure and land use on turtle communities across the eastern United States

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ARTICLE INFO

Keywords:
Landscape heterogeneity
Wetland diversity
Wetland configuration
Turtle
Land use
Abundance

ABSTRACT

Landscape context is integral to population ecology, affecting a range of life history parameters, yet very little is known about how landscape structure influences many taxa. We sampled wetlands at 531 sites across 16 states in the eastern U.S. to examine the influence of landscape heterogeneity and anthropogenic land use on the relative abundance of freshwater turtles, one of the most endangered vertebrate clades in the world. Specifically, we aimed to understand how two components of landscape structure — compositional heterogeneity (wetland diversity) and configurational heterogeneity (wetland aggregation) — influence turtles with varying life history traits. Our results suggest that wetland configuration can modulate the relationship between relative abundance and anthropogenic land use. For example, spotted turtle (*Clemmys guttata*) was negatively associated with hay/

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https://doi.org/10.1016/j.biocon.2023.110088
Received 6 October 2022; Received in revised form 23 February 2023; Accepted 19 April 2023

pasture cover when wetlands were less aggregated, but this relationship subsided as aggregation increased. Notably, the way wetland aggregation modulated land use relationships varied across species. These results suggest that some anthropogenic cover types are not strictly positive or negative for certain species, but are instead context-dependent. Relative abundance also generally increased with higher wetland diversity, indicating the potential importance of landscape supplementation for turtles. We report a range of responses to roads that did not strictly correspond with well-established predictions related to body size and terrestrial activity patterns, including positive associations for certain species. Overall, our study supports the use of context-driven approaches to land use-related conservation and management decisions rather than blanket prescriptions, and further emphasizes that effective conservation of freshwater systems requires a landscape-level perspective.

1. Introduction

Spatial heterogeneity plays an integral role in ecological systems, influencing processes such as movement, competition, predation, population stability, and ecosystem function (Levins and Culver, 1971; Lovett et al., 2005; Oliver et al., 2010; Fahrig, 2017), but little is known about how spatial heterogeneity influences the population ecology of different taxa, including many at-risk species. The spatial structure of a landscape (hereafter referred to as "landscape structure") is generally characterized by two independent components: (1) composition, the number of different cover types and their relative proportions, and (2) configuration, the spatial arrangement of cover types (McGarigal and Cushman, 2002). Heterogeneity in both composition and configuration has been argued as either broadly positive or negative for wildlife (Tews et al., 2004; Fahrig et al., 2011, 2015; Fletcher et al., 2018), but it is clear the ecological effects can be varied and complex (Fahrig, 2017). Therefore, conservation efforts will benefit from an increased understanding of how landscape heterogeneity influences different taxa.

Compositional heterogeneity (i.e., increased number of cover/habitat types) is often expected to benefit populations through landscape complementation or landscape supplementation (Miyashita et al., 2012) — when species utilize different cover types for essential or non-essential resources, respectively (Dunning et al., 1992). For example, greater diversity of cover types may provide foraging, mating, or predator refuge opportunities for different life stages or seasons (Fahrig and Nuttle, 2005). Compositional heterogeneity may play a particularly important role for poikilotherms because a greater diversity of cover may provide a broader range of microclimate refugia and potentially reduce mortality associated with extreme temperatures. However, it may also negatively affect populations if certain cover types are associated with higher mortality or function as ecological traps (Freedberg et al., 2011).

Configurational heterogeneity — generally characterized by an increase in the number and decrease in size of habitat patches, resulting in a greater proportion of edge and often increased isolation of habitat patches (Collinge and Forman, 1998; Fletcher et al., 2018) — has long been considered to negatively affect biodiversity and ecosystems (Haddad et al., 2015) via factors such as edge effects and/or loss of connectivity (Ries et al., 2004; Haddad et al., 2015; Fletcher et al., 2016). However, configurational heterogeneity may also benefit species through positive edge effects (e.g., increased structural diversity; Walter et al., 2009), reduced competition (Levins and Culver, 1971; Collins and Barrett, 1997), and increased landscape complementation (Fahrig and Nuttle, 2005; Slancarova et al., 2014). Indeed, Fahrig (2017) reported that 76 % of examined analyses yielded positive relationships with configurational heterogeneity, demonstrating that the negative effects of habitat configuration cannot be generalized across ecological systems.

Temporal heterogeneity in the availability or condition of cover types can also influence population demographics (e.g., Hodgson et al., 2009). Temporal heterogeneity may negatively affect populations by reducing carrying capacity of individual patches (by affecting amount or quality of resources), reducing connectivity (by eliminating "stepping stone" habitat patches), or increasing exposure to predators and other threats (by spurring movement as individuals emigrate from deteriorating habitat; King, 2014). On the other hand, temporary or ephemeral habitats may benefit certain species by providing refuge from predators or important resources (e.g., foraging opportunities; Milam and Melvin, 2001).

Reptiles are severely underrepresented within the literature regarding the effects of landscape structure (McGarigal and Cushman, 2002; Fahrig, 2017). Filling this knowledge gap — particularly regarding the effect of landscape structure on population demographics — is imperative given the rapid global decline of reptiles (Stanford et al., 2020; Cox et al., 2022). Freshwater turtles are one group of reptiles whose population demographics are likely intimately linked to landscape heterogeneity. Many species are known to, at least temporarily, exploit different wetland habitats throughout the year to forage, thermoregulate, or search for mates (Ernst and Lovich, 2009), suggesting that wetland compositional heterogeneity may have positive population-level effects for many turtles via landscape supplementation.

Freshwater turtles exhibit interspecific variation in upland activity (e.g., Steen et al., 2012) that may potentially render differential responses to configurational heterogeneity of wetlands. Specifically, if terrestrial turtle movement patterns are linked to configurational heterogeneity of wetlands (i.e., more upland movements when configuration is more complex) the degree of configurational heterogeneity may determine the relative vulnerability of populations to threats such as road mortality, agriculture, and predators (Roberts et al., 2023). For example, roads may induce population decline (via road mortality) when wetland configurations are more complex (e.g., many small wetlands) but have limited effect when aggregated (e.g., single large wetland) because there are fewer reasons for individuals to venture as far into the landscape. However, complex wetland configurations may also be beneficial if, for example, they improve the likelihood of hatchlings reaching wetland refuges or provide greater microhabitat/foraging opportunities (Fahrig and Nuttle, 2005). Thus, the effects of landscape structure on turtle demographics are likely varied and complex; contingent upon not only wetland configuration and matrix composition but also life history (Gibbs and Shriver, 2002).

The overarching goal of this study was to investigate the influence of landscape structure on freshwater turtle populations. Our primary aim was to describe the effect of compositional and configurational heterogeneity of wetlands on the relative abundance or freshwater turtle. Our secondary objective was to identify potential relationships between relative abundance and temporal wetland heterogeneity and anthropogenic land use. We expected that relative abundance would be positively associated with compositional heterogeneity for most species due to the benefits of landscape supplementation/complementation (Fig. 1A). We expected that, for species that make more terrestrial inter-wetland movements, there would be an interaction between configurational heterogeneity of wetlands (i.e. the degree of spatial wetland aggregation) and land use such that cover types that may cause mortality (e.g., roads, agriculture, and development) would negatively affect relative abundance at high configurational heterogeneity but have less of an effect at low heterogeneity (Fig. 1B). We expected that species that make fewer terrestrial inter-wetland movements would show minimal or no relationship with these same cover types, regardless of configurational

heterogeneity (Fig. 1B). Due to the threats associated with wetland drying, we expected all species to have lower relative abundance at high proportions of ephemerality and thus, we expected responses ranging from unimodal to negative depending upon whether species tend to be associated with ephemeral wetlands or not (Fig. 1C).

2. Study area and focal species

We sampled wetlands throughout the Atlantic Coastal Plain and Piedmont from southern Maine to northern Florida, with a small proportion of sampling occurring in West Virginia and near Lake Ontario in

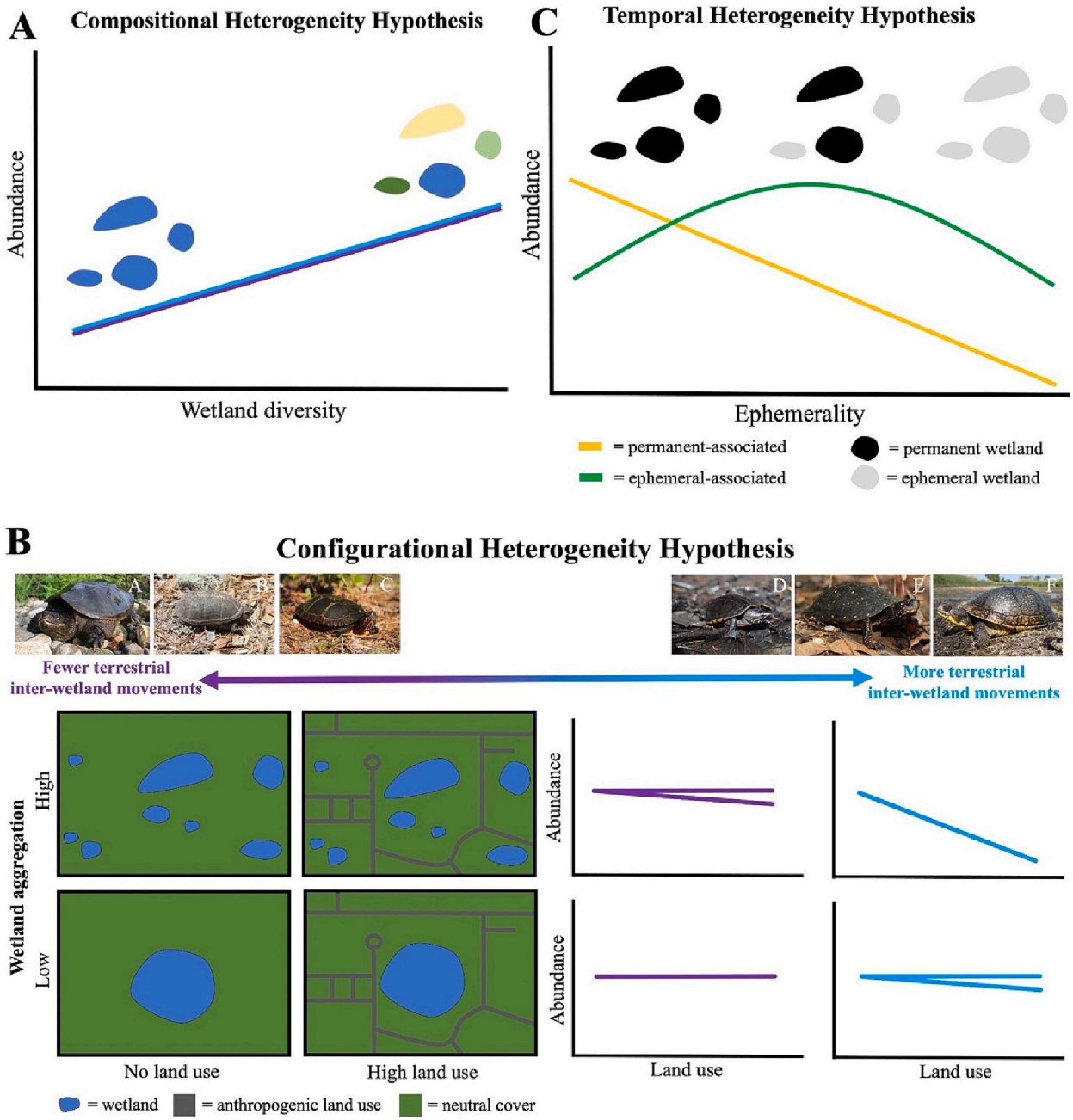


Fig. 1. Illustrations depicting our expectations of relationships with compositional (wetland diversity; A), configurational (wetland aggregation; B), and temporal (ephemerality; C) heterogeneity of wetlands. Our compositional heterogeneity hypothesis (A) stated that species that make more (blue line) and fewer (purple line) terrestrial inter-wetland movements would respond similarly to wetland diversity (different colored polygons represent different wetland types). Our configurational heterogeneity hypothesis (B) stated that the degree of wetland aggregation might modulate relationships with anthropogenic land use types (such as roads, agriculture, and development, which may cause mortality) depending upon propensity for terrestrial inter-wetland movement. We expected abundance of species that make fewer inter-wetland movements to be uninfluenced by land use or display a relatively weak negative relationship at low wetland aggregations. We expected abundance of species that make frequent inter-wetland movements to display no relationship with land use, or a weak negative relationship, at high wetland aggregations, and show strong negative relationships at low wetland aggregation. Our temporal heterogeneity hypothesis (C) stated that species typically associated with permanent wetlands (e.g., painted turtle [*Chrysemys picta*]) would respond negatively to increasing ephemerality (proportion of wetlands that were ephemeral), but that ephemeral-associated species (e.g., spotted turtle [*Clemmys guttata*]) would peak at intermediate levels and decline at high ephemerality. Focal species included snapping turtle (*Chelydra serpentina*; B-A), eastern mud turtle (*Kinosternon subrubrum*; B—B), painted turtle (B—C), striped mud turtle (*Kinosternon baurii*; B—D), spotted turtle (B-E), and Blanding's turtle (*Emydoidea blandingii*; B—F). Photo credit: Michael Jones (B-A, B—C, B—D, B-E, B—F) and Houston Chandler (B—B). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

New York. We do not provide spatially-explicit information due to the vulnerability of turtles to poaching (Sung and Fong, 2018). Focal species for relative abundance analyses included all species that were captured at >15 % of sites within their respective geographic distribution: Blanding's turtle (*Emydoidea blandingii*), snapping turtle (*Chelydra serpentina*), eastern mud turtle (*Kinosternon subrubrum*), painted turtle (*Chrysemys picta*), spotted turtle (*Clemmys guttata*), and striped mud turtle (*K. baurii*). Although the degree to which each of these species make terrestrial inter-wetland movements likely varies, we generally classified painted, snapping, and eastern mud turtle as species that make fewer terrestrial inter-wetland movements and striped mud, spotted, and Blanding's turtle as species that make more inter-wetland movements (Fig. 1B). While each of these species can be captured in certain ephemeral wetlands, depending upon context, we considered Blanding's turtle, spotted turtle, eastern mud turtle, and striped mud turtle to be more ephemeral-associated and painted and snapping turtle to be less ephemeral-associated. We used expert opinion and Ernst and Lovich (2009) to categorize species.

3. Methods

3.1. Collaborative sampling network

Turtle sampling was conducted in association with the Eastern Spotted Turtle Working Group (ESTWG), which is a network of state, nonprofit, academic, federal, and volunteer biologists dedicated to helping conserve the spotted turtle. The ESTWG meets monthly during active projects to coordinate efforts, refine protocols, and track progress in achieving objectives (northeastturtles.org).

3.2. Population sampling

3.2.1. Site selection

We collected data in association with a conservation project focused on spotted turtles, and thus sampling was restricted to the distribution and habitats of this species (i.e., shallow palustrine wetlands, including emergent, shrub, and forested wetlands as well as vernal pools), and results should be interpreted accordingly. Following the ESTWG standardized population monitoring protocol (northeastturtles.org), for each sampling site, we used Google Earth or ArcGIS (Environmental Systems Research Institute, Inc., Redlands, CA) to establish four 200-m radius sampling plots (non-overlapping and separated by up to 400 m) located within target wetlands (hereafter "plots"). We were unable to implement random sampling along a priori environmental or habitat gradients due to the competing objectives of a concurrent project.

3.2.2. Trapping surveys

Within each plot, surveyors placed five collapsible mesh minnow traps (61 × 30.5 cm: ProMar TR-502 or TR-503, Promar, Gardena, CA), totaling 20 per site. When predation risk was deemed high (e.g., due to racoons [*Procyon lotor*] and other mesopredators), we deployed traps lined with wire mesh. In Georgia and Florida, we used wire-based Jones Traps to prevent depredation (Chandler et al., 2017). Jones Traps may have biased sampling against larger individuals for species that reach larger sizes, such as snapping turtle; we address this potential source of bias in the Statistical Analyses Section. Sampling occurred between February and August, but surveyors prioritized sampling in the spring. We attempted to separate traps by at least 30 m, but the exact location of traps within plots were determined by surveyors. We tethered traps to stakes or adjacent structures to prevent movement and inserted floatation devices (plastic bottles or foam floats) into traps to ensure breathing space for turtles during capture. Median water depth when traps were set was 0.26 m. Median distance to the nearest road was 249 m. We deployed traps for four consecutive nights and checked their contents every 24 h. We used canned sardines in oil as bait and rebaited traps every 24 h (rebaiting occurred every 48 h at a very small proportion of sites). We measured air and water temperature at each trap-check. During each trap-check, we recorded the number of each species for each trap. Approximately 26 % of plots were sampled more intensively with two additional 4-day periods for a separate project. Therefore, to eliminate bias associated with increased sampling at these sites, we selected the first 4-day period for inclusion in analyses.

3.3. Environmental covariates

3.3.1. Spatial scales

We calculated land use, wetland, and landscape structure variables at multiple spatial scales (McGarigal et al., 2016), which were categorized into two conceptual levels: "local" and "landscape." Local scales included circular buffers ranging from 30 to 300 m at 30-m increments and were meant to capture the spatial scale of annual or sub-annual movement of the focal species (Ernst and Lovich, 2009). Landscape scales, which included 480-, 960-, 1920-, 3840-, and 7680-m radii were intended to capture larger-scale processes such as dispersal, connectivity, predatory threats (Prange et al., 2004), disturbance regimes, and ecosystem processes (Willey et al., 2022a).

3.3.2. Land use

We calculated all land use variables using the 2016 National Land Cover Database (NLCD) 30-m resolution raster data layers (Yang et al., 2018). Land use variables included mean percent imperviousness, proportion road cover (hereafter referred to as "road density"), proportion hay/pasture cover, and proportion cultivated crop cover (Appendix A). We chose these cover types because they are known or suspected to negatively influence most turtle species (e.g., Stanford et al., 2020; Roberts et al., 2021). We removed commercial cranberry bogs (identified via aerial imagery) from the cultivated crops variable, because this form of agriculture, which is uncommon throughout the study area, can provide suitable wetland habitat for some turtles (unlike other crop types). We estimated imperviousness by taking the mean of all cells within each spatial scale. We estimated the remaining variables by taking the proportion of cells that were classified as road, hay/pasture, or cultivated crops within each spatial scale. We calculated each variable for each spatial scale for all cells in the study area using the Focal Statistics tool in ArcGIS. Last, we extracted cell values for each trap location using the "raster" package (Hijmans, 2019) in R version 4.0.2 (R Development Core Team, 2020) and calculated the mean for all traps within each plot.

3.3.3. Wetland composition and heterogeneity

We used National Wetland Inventory (NWI; U.S. Fish and Wildlife Service [USFWS], 2018) data to calculate 11 wetland variables that can be classified within three categories (Appendix A): wetland amount, ephemerality, and wetland diversity. Wetland diversity and ephemerality metrics represented our measures of compositional and temporal heterogeneity, respectively. The wetland amount category included six variables: the total area of (1) all wetlands excluding those classified as estuarine, (2) shallow palustrine wetlands (those classified as forested, shrub, or emergent), (3) forested wetlands, (4) shrub wetlands, (5) emergent wetlands, and (6) ponds and lakes (Appendix B). We excluded estuarine from the first wetland variable because, while some species may occur in wetlands classified as estuarine, these instances are relatively uncommon and the vast majority of estuarine wetlands are unsuitable for freshwater turtles. The ephemerality category included two variables: proportion of (1) all non-estuarine wetlands that are ephemeral and (2) all shallow palustrine wetlands (i.e., forested, shrub, and emergent) that were ephemeral. We considered wetlands to be ephemeral if they were classified as temporarily flooded, seasonally flooded, or saturated wetlands (Appendix B). The wetland diversity category included three variables: Shannon's Diversity Index (Shannon and Weaver, 1949) for (1) all non-estuarine wetlands, (2) shallow palustrine wetlands, and (3) shallow palustrine wetlands where permanent and

ephemeral wetlands are treated as distinct wetland types (hereafter referred to as "wetland-regime diversity"). We calculated wetland-regime diversity because we suspected that landscapes with a diversity of not only wetland type, but also hydrologic regimes may promote more robust populations of certain species such as spotted turtle and Blanding's turtle. Before calculating each variable in R, we first buffered trap locations in ArcGIS by each spatial scale and measured the area and proportion of each wetland type and hydrological regime.

3.3.4. Wetland configurational heterogeneity

To characterize landscape structure, we rasterized the wetlands surrounding each sampling site using a 30-m cell size and characterized the degree of wetland aggregation using the Aggregation Index (AI), which is defined as the number of alike cell adjacencies divided by the total possible cell adjacencies (McGarigal et al., 2012). Because our goal was to characterize the landscape, we only estimated AI at larger spatial scales of ≥300 m. We calculated AI for all trap locations using the "landscapemetrics" package (Hesselbarth et al., 2019) in R, then averaged values for each spatial scale within plots to produce a single measure of wetland aggregation for each scale and plot. The species examined in this study display varying wetland habitat preferences; therefore, we calculated AI for two different groups of wetland types: (1) all non-estuarine and non-riverine wetlands (painted turtle, snapping turtle, eastern mud turtle, striped mud turtle), and (2) all shallow palustrine wetlands (preferred by spotted turtle, Blanding's turtle). We used expert knowledge and Ernst and Lovich (2009) to assign each species to one of these categories. We did not include riverine habitat because most streams and rivers were not depicted accurately when rasterized with a 30-m cell size. Only two focal species regularly occupy lotic systems within this study area: snapping turtle and eastern mud turtle.

3.4. Statistical analyses

We related relative abundance of plots to environmental covariates using hierarchical closed-population N-mixture models (Royle and Dorazio, 2008) within the "unmarked" package in R (Fiske and Chandler, 2011). This modeling approach uses repeated surveys at individual locations to account for bias associated with imperfect detection (MacKenzie et al., 2002, 2006) to produce relative measures of abundance of unmarked individuals. We used each trap-night as a separate survey to estimate detection probability and account for bias associated with imperfect detection. Closed-population N-mixture models are valid under the assumption of closure where no mortality, immigration, or emigration occur (Royle and Dorazio, 2008). We considered this assumption fulfilled given the narrow temporal window that surveys were conducted, the short daily distances moved by most turtles (e.g., Litzgus and Mousseau, 2004), and high survival rates displayed by turtles (e.g., Congdon et al., 1994). To account for a lack of independence among plots within close proximity, we included "macrosite" as a random effect, which we defined as all plots separated by ≤2 km (a distance that reflected the obvious spatial clustering pattern of plots). We removed nine plots from analyses because wetlands were either not mapped at these locations in the NWI dataset or were situated within large estuarine systems where suitable non-brackish wetlands are exceedingly difficult to identify and delineate. Not all species are fully distributed throughout our study area; therefore, we consulted established species distribution maps (e.g. Ernst and Lovich, 2009) and removed sites clearly falling outside each species' range for respective analyses. While these models aim to estimate abundance, estimates are not perfect, and emphasis should be placed on patterns of relative abundance within species (as is the goal of this study) rather than the magnitude of estimates.

Detection covariates included air temperature, water temperature, day of year, accumulated growing degrees days, an interaction between day of year and growing degrees days, and trap-check visit. We considered air or water temperature because turtles are ectotherms and thus their activity rates are in part influenced by temperature. We considered day of year because turtles can display seasonal activity patterns (Beaudry et al., 2009). We considered growing degrees days because we sampled a broad latitudinal gradient (Appendix C) and suspected detection probability would be higher where annual activity periods are shorter and turtles have less time for activities such as mating, nesting, and foraging (Roberts et al., 2021). We considered an interaction between accumulated growing degrees days and day of year (Roberts et al., 2021) because we suspected the timing of turtle activity (e.g., emergence) may vary with climate. Last, we expected detection could decline with each trap-night due to potential trap avoidance (Hollender et al., 2022). Accumulated growing degrees days (USA National Phenology Network, 2020) represented the number of degrees the average daily temperature was above 50° F summed across the entire year. We scaled continuous variables such that mean = 0 and SD = 1 to improve model convergence.

We used Akaike's Information Criterion corrected for small sample size (AICc; Burnham and Anderson, 2002) to compare the performance of candidate models. First, to determine the most appropriate probability distribution for each species analysis, we compared zero-inflated Poisson and negative binomial distributions while also including a set of arbitrarily selected detection and site covariates to account for additional variation. The best performing distribution was used in all subsequent models.

We a priori determined a subset of the environmental variables that would be considered for each species (Appendix D). Because Blanding's turtle and spotted turtle are primarily associated with palustrine wetlands, we did not consider wetland "amount", "diversity", and "ephemerality" variables that included all wetlands (Appendix A), or the amount of pond habitat. Similarly, we did not consider variables that only included shallow palustrine wetlands for other species. We used expert opinion and Ernst and Lovich (2009) to group these species. We did not consider land use types if they were not present at any plots or only present at very low levels. To avoid overfitting models, we a priori established a target number of detection, wetland, and land use covariates that would be allowed in any model for each species (Appendix E). We only allowed the number of covariates to exceed these numbers in cases where a land use-aggregation interaction was present in top models. We considered variables correlated if $r > 0.7$ and removed the variable with the higher AICc value when comparing single-variable models.

To begin the model selection process, we first used the "MuMIN" package (Barton, 2016) in R to select detection covariates by comparing all variable subsets within the maximum number of detection covariates allowed for that species (Appendix E). We considered quadratic terms for air temperature, water temperature, and day of year. We selected the detection covariates with the lowest AICc score and included these within all subsequent models.

We expected that wetland characteristics would be most important in predicting relative abundance, and land use variables of secondary importance. Furthermore, we expected that accounting for variation associated with wetland characteristics would be important in elucidating land use relationships. Therefore, we first selected the best combination of wetland variables (using AICc) and held these variables constant within models while selecting land use covariates.

Prior to wetland variable selection, we first determined the best performing spatial scale (McGarigal et al., 2016) for each wetland variable. We considered both linear and quadratic terms during scale selection. We selected the scales with the lowest AICc value. If no scale performed better than the null model, that variable was not considered for model selection. We did not have a priori expectations regarding which wetland variable combinations would perform best but wanted to avoid generating the large number of models that would be created by comparing all variable subsets. Thus, we followed a process similar to other studies (Roberts and King, 2017; Roberts et al., 2021) that sequentially considered the best performing variables within each

category of wetland variables: (step 1) compare all subsets of "wetland amount" variables and select the best combination, (step 2) compare all subsets of variables when considering "ephemerality" variables and those from step one and select the best combination, and finally (step 3) compare all subsets of variables when considering "wetland diversity" variables and those from step two and select the best combination. This process limits the number of model comparisons while allowing each variable to be considered. The order of these steps was chosen arbitrarily.

Prior to land use variable selection, we again determined the best performing spatial scale for each variable while retaining selected wetland variables in all models. During scale selection, we considered linear terms as well as interactions between linear terms and wetland aggregation at the same scale (e.g., interaction between road density within 300 m and AI within 300 m). We also considered a model with AI alone, if models with interaction terms performed best, but the CI of the interaction coefficient did not overlap 0 (suggesting that the linear AI term was driving model importance). Last, we compared all subsets of land use variable combinations. We report all models with ΔAICc <2 and considered covariates that occurred within these models strongly supported if 95 % confidence intervals (CI) of coefficient estimates did not overlap zero (Chandler et al., 2009).

We examined the potential effect of Jones Traps on snapping turtle abundance analyses by removing samples from Georgia and Florida (where they were used) and rerunning models. We found no substantive change in results (i.e., coefficients and CI remained similar) and therefore reported results for analyses of the entire range.

4. Results

We recorded 4930 detections of 12 turtle species across 531 plots from 2018 to 2020. We conducted surveys in the Maine (21 plots), New Hampshire (42), Vermont (8), Massachusetts (68), Rhode Island (16), New York (33), New Jersey (8), Pennsylvania (46), Delaware (19), Maryland (23), District of Columbia (3), West Virginia (24), Virginia (52), South Carolina (42), Georgia (75), and Florida (51). We sampled across 5 Environmental Protection Agency Level Two Ecoregions and 11 Level Three Ecoregions. There were two primary geographic gaps in our sampling within the spotted turtle distribution in the study area, including North Carolina (335 km between nearest sampling locations) and between northern New Jersey and northern Connecticut (238 km). Sampling ranged 28.1–44.4 degrees latitude (Appendix C). Six of the 12 species detected had sufficient sample sizes (>15 %, Appendix E) within their geographic distribution for analysis: Blanding's turtle (21 of 66 plots), snapping turtle (143 of 522), eastern mud turtle (127 of 281), painted turtle (201 of 354), spotted turtle (188 of 522), and striped mud turtle (62 of 200). Six additional species were captured but excluded from analyses due to insufficient sample size (<15 % of sites; Appendix E): pond slider (*Trachemys scripta*), eastern musk turtle (*Sternotherus odoratus*), wood turtle (*Glyptemys insculpta*), northern red-bellied cooter (*Pseudemys rubriventris*), Florida soft-shelled turtle (*Apalone ferox*), and loggerhead musk turtle (*S. minor*).

In line with our expectations, most species (all except the eastern mud turtle), increased in abundance with increasing compositional heterogeneity as measured by diversity of wetland types (Table 1, Fig. 2). Spotted turtle and painted turtle displayed unimodal relationship with wetland-regime diversity and diversity of all wetlands respectively. In contrast with our expectation, no species displayed unimodal relationships with wetland ephemerality. Painted turtle displayed a strong negative relationship with ephemerality, while eastern mud and spotted turtle displayed strong positive relationships (Table 1). There were only six relationships with wetland amount (across four species) within top models, four of which appeared at the 30-m scale (Table 1).

Three of six species displayed strong interactive relationships between anthropogenic land use and configurational heterogeneity, as measured by wetland aggregation (Table 2, Fig. 3), although not all species followed the relative abundance patterns we expected. In line with our expectations, spotted turtle showed a negative relationship with hay/pasture cover at low aggregations, and this negative relationship subsided as wetlands became more aggregated (Fig. 3A,C, Appendix F). Spotted turtle abundance was positively associated with proportion crop cover at high aggregations, but error associated with this relationship was very large (Appendix F). In contrast to our expectations, snapping turtle displayed a positive relationship with cultivated crop cover at lower aggregations and no apparent relationship at higher wetland aggregations (Table 2, Fig. 3B, E; Appendix F). Striped mud turtle displayed a negative relationship with cultivated crop cover across all aggregations, but the pattern was somewhat more pronounced at higher aggregations (Fig. 3D; Appendix F). Four species exhibited strong relationships with road density, but the direction of this relationship ranged from negative (spotted turtle and eastern mud turtle) to positive (snapping turtle and striped mud turtle; Table 2; Fig. 4). Eastern mud turtle exhibited a strong negative relationship with cultivated crop cover (Table 2). Painted turtle and eastern mud turtle showed strong positive and negative relationships with wetland aggregation respectively (Table 2). Detection was not the focus of this study and therefore we report detection coefficients in Appendix G.

Table 1
Parameter estimates (standard error) for wetland variables of best performing models of turtle relative abundance. Numbers associated with covariates indicate spatial scale (m). Squared terms indicate quadratic relationships and bold coefficients indicate strong relationships. See Table 2 for land use variables included within each model as well as delta AICc values and model weights.

Species		Amount (area)		Ephemerality		Diversity	
Blanding's turtle	Covariates						Wetland-regime 960
	Model 1						**0.968 (0.364)**
Spotted turtle	Covariates				Shallow palustrine 7680	Shallow palustrine 30	Wetland-regime 480^2
	Model 1				**1.356 (0.296)**	**0.250 (0.1)**	**−0.269 (0.095)**
	Model 2				**1.384 (0.291)**	**0.236 (0.098)**	**−0.262 (0.093)**
	Model 3				**1.35 (0.294)**	**0.252 (0.1)**	**−0.271 (0.095)**
Painted turtle	Covariates		Forest 30	All wetland 180		All wetland 960	
	Model 1		**−0.4 (0.119)**	**−0.363 (0.116)**		**−0.444 (0.126)**	
Snapping turtle	Covariates	All wetland 960^2	Pond 30^2			All wetland 60	
	Model 1	**−0.266 (0.116)**	**−0.079 (0.038)**			**0.215 (0.083)**	
	Model 2	**−0.261 (0.115)**	**−0.077 (0.038)**			**0.216 (0.083)**	
Eastern mud turtle	Covariates	Forest 30	Emergent 30	All wetland 1920			
	Model 1	**−0.218 (0.109)**	**−0.303 (0.101)**	**0.638 (0.179)**			
Striped mud turtle	Covariates	Emergent 960				All wetland 1920^2	
	Model 1	**0.34 (0.154)**				**0.342 (0.116)**	
	Model 2	**0.376 (0.152)**				**0.277 (0.105)**	

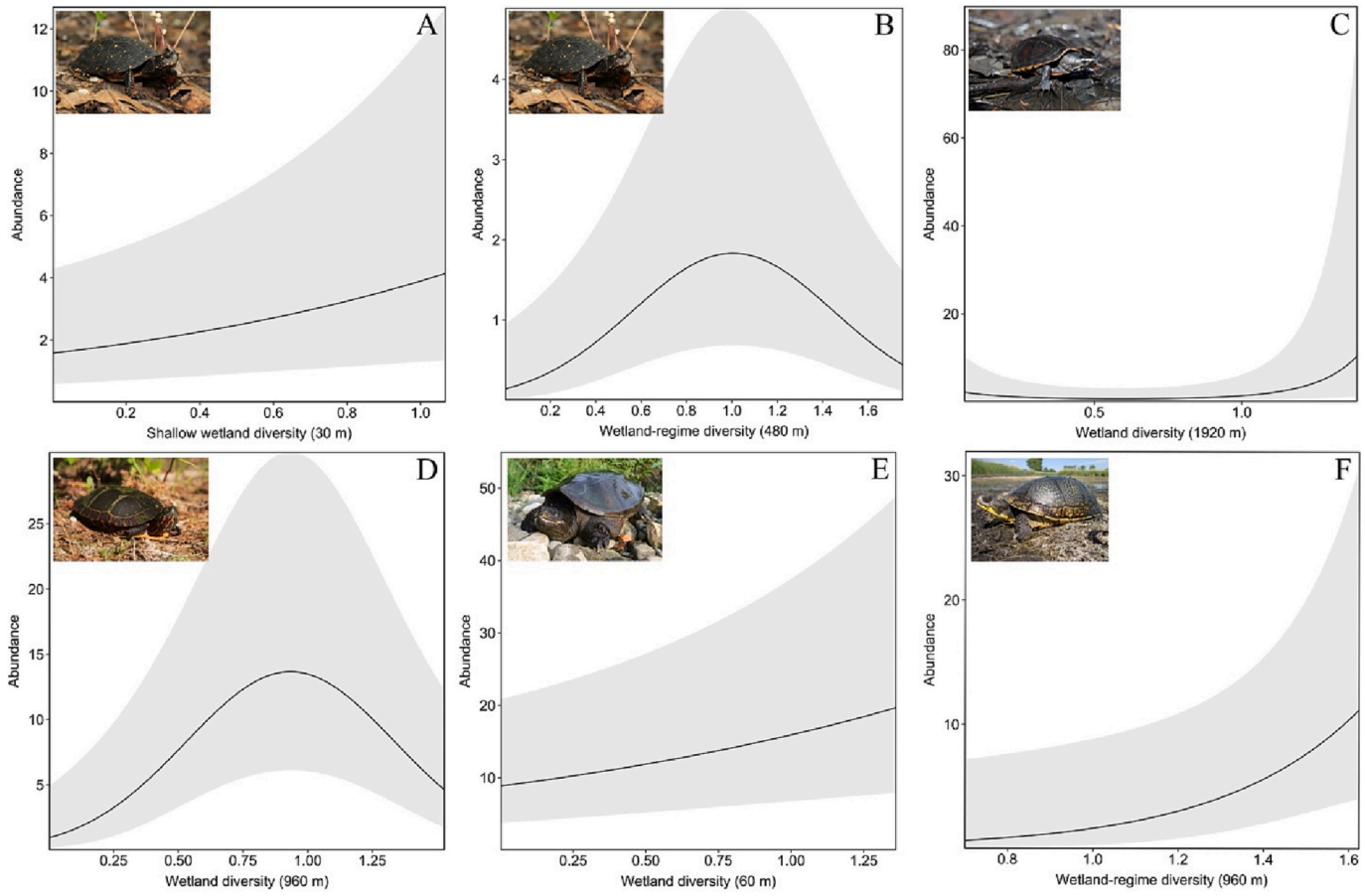


Fig. 2. Predicted relative abundance in relation to wetland diversity for spotted turtle (A, B), striped mud turtle (C), painted turtle (D), snapping turtle (E), and Blanding's turtle (F). "Wetland-regime diversity" represents a metric reflecting the diversity of wetlands when ephemeral wetland types are considered separately from permanent wetlands. Gray areas indicate 95 % confidence intervals. Photo credit: Michael Jones.

Table 2
Parameter estimates (standard error) for land use variables of best performing models of turtle relative abundance. Numbers associated with covariates indicate spatial scale (m). Bold coefficients indicate strong relationships. See Table 1 for wetland variables included within each model. AI refers to the Aggregation Index.

Species		Land use						ΔAICc	weight
Blanding's turtle	Covariates	Impervious 270							
	Model 1	−0.742 (0.448)						0	1
Spotted turtle	Covariates	Road density 960	Cultivated crops 60	Hay 480	Aggregation index 480	Interaction: hay*AI	Impervious 30		
	Model 1	**−0.417 (0.131)**	−0.878 (0.493)				−0.524 (0.306)	0	0.43
	Model 2	**−0.437 (0.126)**	−0.8537 (0.484)	−0.097 (0.124)	0.208 (0.139)	**0.371 (0.17)**		0.28	0.38
	Model 3	**−0.467 (0.128)**	−0.87 (0.496)					1.68	0.19
Painted turtle	Covariates	Aggregation index 300							
	Model 1	**0.381 (0.126)**						0	1
Snapping turtle	Covariates	Road density 960	Cultivated crops 7680	Aggregation index 7680	Interaction: crops*AI	Hay 30			
	Model 1	**0.219 (0.084)**	0.132 (0.11)	0.115 (0.129)	**−0.265 (0.121)**			0	0.63
	Model 1	**0.219 (0.083)**	0.136 (0.11)	0.084 (0.132)	**−0.269 (0.121)**	−0.089 (0.092)		1.06	0.37
Eastern mud turtle	Covariates	Road 1920	Cultivated crops 1920	Aggregation index 300					
	Model 1	**−0.89 (0.257)**	**−0.453 (0.176)**	**−0.279 (0.101)**				0	1
Striped mud turtle	Covariates	Road 60	Cultivated crops 1920	Aggregation index 1920	Interaction: crops*AI	Impervious 1920			
	Model 1	**0.365 (0.132)**	−0.783 (0.433)	0.006 (0.305)	**−0.92 (0.335)**			0	0.72
	Model 2	**0.362 (0.135)**				−1.262 (0.892)		1.86	0.28

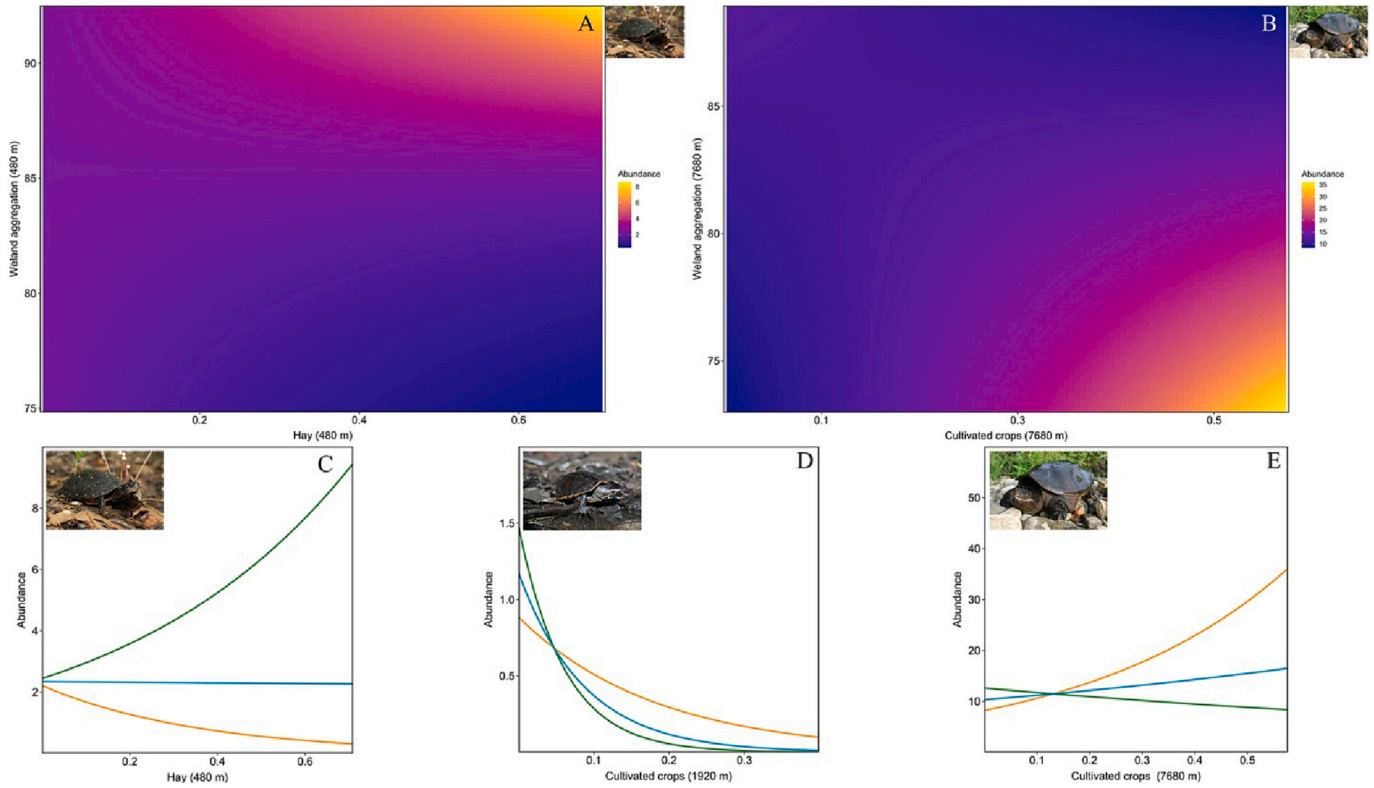


Fig. 3. Predicted relative abundance in relation to land use types at varying levels of wetland aggregation (orange lines = 0.25 quantile, blue lines = median, green lines = 0.75 quantile of aggregation) for spotted turtle (A, C), snapping turtle (B, E), and striped mud turtle (D). Confidence intervals are excluded to reduce plot complexity and aid visual interpretation, but can be viewed in Appendix F. Error associated with spotted turtle (C) abundance at high aggregations was large and should therefore be interpreted with added caution. Photo credit: Michael Jones. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

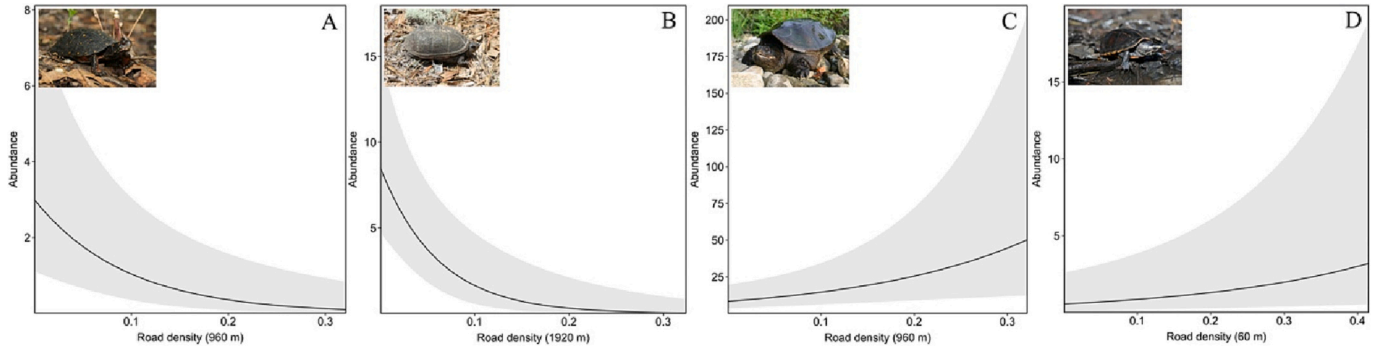


Fig. 4. Predicted relative abundance in relation to roads for spotted turtle (A), eastern mud turtle (B), snapping turtle (C), and striped mud turtle (D). Gray areas indicate 95 % confidence intervals. Photo credit: Michael Jones (A,C,D) and Houston Chandler (B).

5. Discussion

5.1. Compositional heterogeneity

This study provides evidence that turtle populations are more abundant where there is greater diversity of wetland types. Only one species (eastern mud turtle) did not show a positive association between relative abundance and wetland diversity. The generality of this relationship suggests that landscape supplementation likely plays an important role in turtle population demographics throughout eastern North America and perhaps elsewhere. Increased wetland diversity may benefit turtles by providing greater ecotone/edge density for thermoregulation or by providing different life-history needs (e.g., spring foraging pools and over-wintering wetlands). Diverse wetland systems may also indirectly benefit turtles through synergistic effects that, for example, may influence resource availability. If anthropogenic activities tend to homogenize wetland systems, it is possible this pattern instead reflects a tendency for turtles to be less abundant where humans are more common; however, this is unlikely given that wetland diversity was uncorrelated with any anthropogenic land use types.

Larger populations tend to be more stable (Oliver et al., 2010), suggesting that wetland diversity may confer population resilience to stochastic environmental extremes. In addition to promoting turtle abundance, wetland diversity may also provide more microrefugia during extreme temperatures or drying events that can buffer against mortality among adults and juveniles (Robertson et al., 2021). Therefore, our findings suggest that conservation planners (e.g., Jones et al., 2018; Willey et al., 2022b) should consider conserving, or even

increasing, wetland diversity to not only curb contemporary population declines, but also promote climate change resilience (Oliver et al., 2010; Robertson et al., 2021). This may mean focusing on restoring and maintaining important disturbance regimes and other processes that generate wetland heterogeneity, such as beaver (*Castor canadensis*) and muskrats (*Ondatra zibethicus*; Kua et al., 2020), seasonal flooding (Wright et al., 2015), and wetland succession (Wilson, 2002).

Given that we restricted sampling to shallow palustrine wetlands, it is possible that a portion of these results simply reflect the fact that, in order to occupy these wetland types, certain species also need their preferred wetlands nearby. For example, painted turtle might be associated with wetland diversity because this is where deeper pond habitat is available. However, if this were the case, we would expect the amount of pond habitat to appear within top models instead of wetland diversity; it did not. Moreover, many of the focal species in this study are not associated with individual wetland types but rather a range of finer microhabitat conditions (Anthonysamy et al., 2014). This is further indicated by the fact that the proportion of sites at which species were captured was similar to that of the spotted turtle, the focal species for sampling.

5.2. Configurational heterogeneity

Our findings suggest that habitat configuration can modulate the relative effect of certain anthropogenic cover types on relative abundance, although patterns did not always follow expectations nor strictly correspond with species movement characteristics (Fig. 1C). The spotted turtle, which is characterized by terrestrial inter-wetland movements (Milam and Melvin, 2001), displayed negative associations with hay/pasture cover at low wetland aggregation within 480 m, suggesting that populations may experience increased mortality rates via machinery (Saumure et al., 2007; Roberts et al., 2021) and/or predators (Harding, 1985) during inter-wetland movements when wetlands are spatially disaggregated. This relationship subsided at intermediate aggregations, suggesting that the threat of these cover types lessens as terrestrial movements become shorter or less frequent due to increased wetland aggregation. Interestingly, abundance appeared to be positively associated with these anthropogenic cover types at high aggregation (although the standard error was large; Appendix F), suggesting the possible benefit of anthropogenic activities (e.g., nesting or thermoregulatory opportunities) if sources of mortality are minimized (although further research is needed). Indeed, studies commonly report positive associations with land use types presumed to cause mortality (e.g., Winchell and Gibbs, 2016; Paterson et al., 2019). Therefore, our results suggest that some anthropogenic cover types may not be strictly negative for certain species but in fact context-dependent. This possibility should not be misinterpreted as an opportunity to relax concern about these threats but rather a reminder that the suite of factors that influence turtle demographics is complex, and in some cases, populations might be more stable than landscape composition alone might suggest.

Notably, two species displayed interactions between aggregation and land use, but deviated from our expectation in different ways. The snapping turtle, which we expected to be relatively uninfluenced by wetland configuration due to its tendency to make fewer terrestrial inter-wetland movements relative to other species (Steen et al., 2010), showed the opposite trend of that exhibited by spotted turtle — a positive relationship with cultivated crop cover at low aggregations that subsided and became slightly negative at higher aggregations. Snapping turtles are known to nest within crop fields (Thompson et al., 2018), and therefore abundance could be greater with higher cultivated crop cover if more spatially dispersed wetland habitat provides hatchlings with more accessible refugia from predators immediately post-hatching. It should be noted that crops may negatively influence snapping turtle nest success or hatchling condition (Thompson et al., 2018), although it is not clear if these effects are widespread. A more complex arrangement of wetlands may also make it more challenging for predators to find nests (Marchand and Litvaitis, 2004a). In contrast, the more terrestrial striped mud turtle displayed a negative relationship with cultivated crop cover in all cases, but this relationship was less pronounced when wetlands were less aggregated. Because striped mud turtles are considerably more terrestrial than snapping turtles, they might be vulnerable to agricultural machinery and associated predators regardless of wetland configuration; however, since they often use terrestrial habitat to aestivate during periods of wetland drying, landscapes with less aggregated wetlands may provide more and closer refugia during machinery use, acting to lessen the negative affect. It should be noted that the error associated with lower aggregations was high (Appendix F) and thus caution should be exercised when considering the biological significance of this relationship. These results highlight the complex range of effects that wetland aggregation may have across species, and further emphasizes the need to account for, or at least thoroughly describe, habitat configuration, when examining the effect of land use on populations.

Landscape configuration may help to explain differences in results among studies (Roberts et al., 2023). For example, several studies have linked male-skewed sex ratios to higher road densities (Steen and Gibbs, 2004; Marchand and Litvaitis, 2004b; Aresco, 2005; Steen et al., 2006), which has kindled the notion that this phenomenon is ubiquitous. However, other studies have found no such relationship (e.g., Dorland et al., 2014; Hamer et al., 2016; Carstairs et al., 2018; Vanek and Glowacki, 2019) or even the opposite trend (Buchanan, 2017; Bowne et al., 2018) for the same species. While there is very little doubt that roads (and other cover types) can skew sex ratios, it is possible that these seemingly conflicting results could be collectively explained by the possible modulatory effect of wetland configuration.

5.3. Roads

With this large, collaborative study, we provide insight into the effect of roads on the relative abundance of several turtle species. Roads are frequently cited as a leading threat to turtles (Steen and Gibbs, 2004; Steen et al., 2012), yet the wealth of research examining the effect of roads is largely equivocal (Dorland et al., 2014). Most studies report no effect of roads on turtle occurrence (e.g., Quesnelle et al., 2013; Buchanan et al., 2019; Paterson et al., 2021), and few have linked abundance to roads (although see Rizkalla and Swihart, 2006, Roberts et al., 2021), despite efforts to do so (Steen and Gibbs, 2004; Marchand and Litvaitis, 2004b; Beaudry et al., 2008; Dorland et al., 2014; Hamer et al., 2016). Our findings support the notion that roads are detrimental to some turtle species but suggest the magnitude of this threat may vary across species.

We observed that both the spotted turtle and eastern mud turtle were strongly negatively associated with road density, which was expected given that both species are relatively terrestrial (Milam and Melvin, 2001; Harden et al., 2009). In contrast, snapping turtle and striped mud turtle both displayed positive relationships with road density (960 and 60 m respectively). Positive associations with roads (Paterson et al., 2021) and urbanization (Winchell and Gibbs, 2016) have been observed for snapping turtles. Snapping turtles are highly aquatic and thus may have lower exposure to cars compared to more terrestrial species. Certain roadside wetlands may also have longer hydroperiods (due to digging during road construction), which may provide refugia to turtles during drought. Roadsides are also known to attract nesting females (Murphy et al., 2022), and, if roads also act to deter or limit populations of nest predators, they may facilitate ecological release, allowing greater reproductive success than would otherwise be possible (Rytwinski and Fahrig, 2012). Indeed, Murphy et al. (2022) found that artificial nests along roads experienced less predation than nonroad nests, and that this reduction could compensate for road-associated mortality in painted turtle populations (also see Knoerr et al., 2021).

Gibbs and Shriver (2002) simulated road mortality throughout the eastern United States, finding that turtles they classified as “large-bodied” (*Chelydra*) and “semi-terrestrial” (*Clemmys*, *Glyptemys*,

Emydoidea) species were negatively affected by road networks, while "small-bodied pond turtles" (*Chrysemys*, *Pseudemys*, *Trachemys*, and *Kinosternon*) were unaffected. After 20 years, this study remains one of the most frequently cited studies related to the effect of roads on turtles, and its predictions are often assumed to occur in real populations, despite a dearth of empirical evidence. Our results show only partial agreement (two of six species), with only spotted turtles (semi-terrestrial) and painted turtles (small-bodied) following the predictions of Gibbs and Shriver (2002). These discrepancies might reflect the fact that Gibbs and Shriver (2002), as they discuss, only modeled nesting-related movements without considering other potentially important terrestrial movements associated with dispersal, inter-wetland travel, aestivation, and brumation. For example, while eastern mud turtles typically only occupy a single wetland within a year and make relatively short nesting movements (Steen et al., 2012), they also exhibit considerable terrestrial activity associated with aestivation and brumation (Harden et al., 2009), likely increasing their relative vulnerability and potentially explaining the negative association we observed. However, terrestrial activity alone cannot explain the full range of our results (e.g., positive associations), emphasizing the complexity of wildlife-road relationships (Rytwinski and Fahrig, 2012). These findings highlight that caution should be exercised when drawing broad conclusions about potential threats to turtles.

We were unable to account for several characteristics of roads that may influence their relative effect on turtles. For example, roads vary in surface type, sinuosity, speed limit, traffic volume, and juxtaposition with respect to wetland habitat (among other characteristics), which may interact with species traits (e.g., body size, walking speed, site fidelity, home range size) to influence road mortality or other factors that affect populations. It is possible that, if accounted for, these characteristics might explain some of the error associated with our results as well as the variation in patterns observed among species.

5.4. Temporal heterogeneity

In contrast with our expectation (Fig. 1B), two species often associated with ephemeral wetlands, the eastern mud turtle and spotted turtle, displayed strong positive relationships with ephemerality at 1920 m and 7680 m respectively. Notably, these scales are substantially larger than the typical eastern mud turtle or spotted turtle home range (e.g., Milam and Melvin, 2001; Harden et al., 2009), suggesting that the benefits conferred by wetland ephemerality may reflect population-, metapopulation-, or ecosystem-level processes. Since ephemeral wetlands are among the most vulnerable to human activity (Dahl, 1990; Calhoun and de Maynadier, 2008), landscapes with high ephemerality may also reflect ecosystems that are less disturbed and more functionally intact. In contrast, painted turtle, which displayed a negative relationship with ephemerality, responded at a scale similar or smaller than its typical home range size (Rowe and Dalgarn, 2010), likely reflecting their tendency to avoid ephemeral wetlands at the scale of individual habitat selection.

5.5. Caveats

When considering these findings, it is important to remember that we targeted spotted turtle habitats (shallow palustrine wetlands), which may have introduced biases. For example, if pond quality is disproportionately affected by roads, we might have observed a positive association with roads for the snapping turtle (which is often pond-associated), if, in response, they select more shallow wetlands. However, we believe it is more likely that such species would emigrate or simply decline in abundance in response to increased road density. While spotted turtles largely occur within shallow wetlands, they are otherwise generalist in nature and occupy a range of microhabitat and wetland conditions that other species, with varying habitat preferences, also occupy. Therefore, we believe our study is akin to other studies that sample communities within a given cover type (e.g., mature forest) and detect species that readily occur within that cover type, but generally vary in habitat and landscape requirements. This important sampling restriction should be considered if applying these findings to other habitats and contexts.

While the use of smaller traps allowed us to access remote areas, and therefore substantially increase our sample size, they likely biased our capture data toward smaller individuals of species that can reach large sizes, such as snapping turtle. In particular, there was increased bias against large individuals of these species in Georgia and Florida where, in order to protect against predators, Jones Traps were deployed variably across sites. While our assessment of this potential bias indicated no effect of Jones Traps, caution should nevertheless be exercised when applying these findings elsewhere.

Another potential factor to consider is the potential for population responses to temporally lag behind land use establishment. Because most turtles exhibit long life spans and individuals can potentially remain within landscapes long after habitat degradation has occurred, populations may not display substantive declines in abundance for many years. These "disconnects" may mean that certain relationships not observed in this study could become apparent over time (e.g., negative relationships with roads).

Last, a limitation of the Aggregation Index (AI) is that it can be correlated with habitat amount (Neel et al., 2004), which was the case in this study. Aggregation Index was correlated with wetland amount for the three species that displayed strong interactions: spotted turtle ($r = 0.712$), striped mud turtle ($r = 0.763$), and snapping turtle ($r = 0.786$). Therefore, we cannot definitively rule out that habitat amount may have contributed in some way to these results. However, turtle populations (and reptiles more broadly) generally do not show the area relationships observed for other taxa (Prugh et al., 2008; Quesnelle et al., 2015), which is supported by our results. Moreover, it would be challenging to explain the range of interaction relationships involving AI if habitat amount were the primary driver. Thus, we believe these patterns are more likely driven by wetland configuration.

6. Conclusion

With this study, we provide insight into the role that landscape heterogeneity and anthropogenic land use play in shaping turtle populations across the eastern United States. To our knowledge, this is the first evidence that wetland diversity (i.e., compositional heterogeneity) generally promotes turtle abundance, suggesting that prioritizing the protection of landscapes harboring high wetland diversity at multiple scales will broadly benefit turtles (Roe and Georges, 2007). This finding also implies that the destruction or degradation of wetlands not critical to the survival of a certain species may still trigger decline. In contrast, configurational heterogeneity of wetlands appears to influence species in strikingly different ways, most notably by modulating relationships with anthropogenic cover types such that abundance may increase or decrease depending upon the relative aggregation of wetlands. Therefore, for some species, certain land use types may not be strictly "bad" or "good" but dependent upon landscape context. Moreover, conservation strategies that mitigate the effects of specific land uses (e.g., altering mowing regimes or fencing roads) may be less urgent at certain levels of wetland aggregation. Our findings help to fill key conservation and management knowledge gaps regarding the influence of landscape structure on freshwater turtles (McGarigal and Cushman, 2002; Quesnelle et al., 2013), one of the most endangered clades in the world (Lovich et al., 2018; Stanford et al., 2020).

Finally, our study further contextualizes the impact that humans have had on turtle populations in the United States. Since European colonization, >53 % of wetlands have been lost throughout the conterminous United States, including roughly 11 million acres — approximately the area of Massachusetts, Connecticut, and Rhode Island combined — of palustrine wetlands (Dahl, 1990; Wilen and Frayer,

1990). This torrent of wetland destruction most likely led to both widespread loss of wetland diversity and increased configurational heterogeneity, which — coupled with the rapid expansion of agriculture, development, and road networks within the intervening upland matrix — almost certainly facilitated greater declines than those explained by habitat loss alone. Importantly, our results provide strong support for the now decades-old, but undervalued notion that effective conservation of freshwater species and communities requires a shift away from individual and buffered-based wetland conservation to multi-scale landscape-level conservation (Roe and Georges, 2007; Sawatzky and Fahrig, 2019).

CRediT authorship contribution statement

H. Patrick Roberts: Investigation, Conceptualization, Methodology, Data curation, Formal analysis, Writing – original draft, Writing – review & editing, Visualization, Project administration, Funding acquisition. **Lisabeth L. Willey:** Conceptualization, Investigation, Methodology, Supervision, Writing – review & editing, Project administration, Funding acquisition. **Michael T. Jones:** Conceptualization, Investigation, Methodology, Writing – review & editing, Project administration, Funding acquisition. **David I. King:** Funding acquisition, Supervision, Writing – review & editing. **Thomas S.B. Akre:** Investigation, Writing – review & editing, Funding acquisition. **John Kleopfer:** Investigation, Methodology, Writing – review & editing, Project administration, Funding acquisition. **Donald J. Brown:** Investigation, Writing – review & editing, Methodology. **Scott W. Buchanan:** Investigation, Writing – review & editing, Methodology. **Houston C. Chandler:** Investigation, Writing – review & editing. **Phillip deMaynadier:** Methodology, Writing – review & editing, Funding acquisition. **Melissa Winters:** Investigation. **Lori Erb:** Investigation, Methodology, Writing – review & editing, Funding acquisition. **Katharine D. Gipe:** Investigation, Methodology, Writing – review & editing, Funding acquisition. **Glenn Johnson:** Investigation. **Kathryn Lauer:** Investigation, Data curation. **Eric B. Liebgold:** Investigation, Writing – review & editing. **Jonathan D. Mays:** Investigation, Methodology, Writing – review & editing, Funding acquisition. **Jessica R. Meck:** Investigation. **Joshua Megyesy:** Investigation, Methodology, Funding acquisition. **Joel L. Mota:** Investigation, Writing – review & editing. **Nathan H. Nazdrowicz:** Investigation, Writing – review & editing. **Kevin J. Oxenrider:** Investigation, Methodology. **Molly Parren:** Investigation, Data curation, Project administration. **Tami S. Ransom:** Investigation, Writing – review & editing. **Lindsay Rohrbaugh:** Investigation. **Scott Smith:** Investigation. **Derek Yorks:** Investigation, Writing – review & editing, Methodology, Funding acquisition. **Brian Zarate:** Investigation, Funding acquisition.

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.

Acknowledgments

We would like to thank the many biologists who contributed to data collection, without which this project would not have been possible. We would also like to thank the numerous landowners who granted access for population sampling. Our reviewers provided thoughtful and thorough comments that we believe substantially improved the manuscript. This work was funded by the Northeast Regional Conservation Needs Grant Program (RCN Grant 2017-00; rcngrants.org) and a Competitive State Wildlife Grant award (F18AP00182) from the U.S. Fish and Wildlife Service (USFWS) to 12 active partners including Virginia Department of Game and Inland Fisheries, Smithsonian Conservation Biology Institute, American Turtle Observatory, Connecticut Department of Energy and Environmental Protection, District of Columbia Department of Energy & the Environment, Fisheries and Wildlife Division; Georgia Department of Natural Resources, The Orianne Society, Maine Department of Inland Fisheries and Wildlife, Massachusetts Division of Fisheries and Wildlife, New Hampshire Fish and Game Department, Pennsylvania Fish and Boat Commission, The Mid-Atlantic Center for Herpetology and Conservation, and West Virginia University. H. Patrick Roberts was partially supported by a Natural Resources Conservation Service grant award (NR193A750023C003). Additional funding was provided by the U.S. Fish and Wildlife Service to The Orianne Society (F15AC00965 Modification 3). The West Virginia Division of Natural Resources provided additional funding. Donald Brown was supported by the USDA National Institute of Food and Agriculture, McIntire Stennis project WVA00820, the West Virginia Agricultural and Forestry Experiment Station, and the USDA Forest Service Northern Research Station. Any use of trade, product, website, or firm names in this publication is for descriptive purposes only and does not imply endorsement by the U.S. Government.

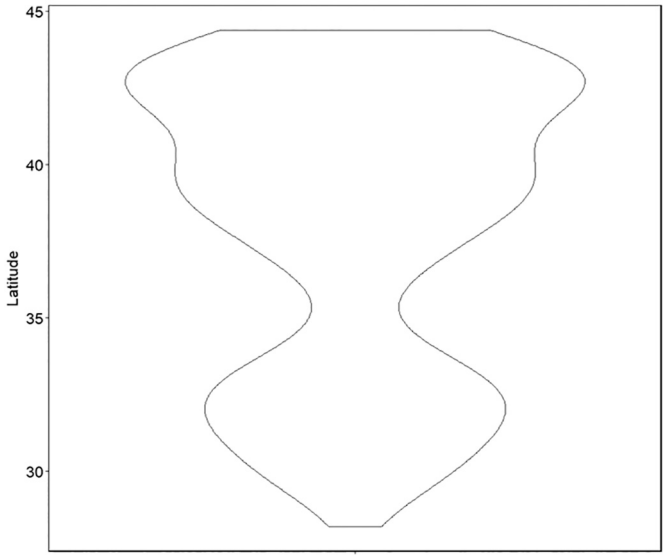
Appendix A. Environmental covariates considered within analyses of relative abundance

Class	Metric	Cover Type
Wetland	Area (ha)	All wetland types (excluding estuarine and marine)
Wetland	Area (ha)	Shallow palustrine wetlands (emergent, shrub, forested)
Wetland	Area (ha)	Forested wetlands
Wetland	Area (ha)	Shrub wetlands
Wetland	Area (ha)	Emergent wetlands
Wetland	Shannon's Diversity	All wetlands
Wetland	Shannon's Diversity	Shallow palustrine wetlands (emergent, shrub, forested)
Wetland	Shannon's Diversity	Wetland-Regime
Wetland	Proportion of wetlands	Ephemeral wetlands
Land Use	Mean cell value	Imperviousness
Land Use	Proportion	Roads
Land Use	Proportion	Hay/pasture
Land Use	Proportion	Cultivated crops
Landscape Structure	Aggregation Index	Wetland

Appendix B. Definitions of wetland and hydroperiod types from the National Wetland Inventory

Category	Type	Definition
Wetland	Forested	The Class Forested Wetland is characterized by woody vegetation that is 6 m tall or taller. All water regimes are included except subtidal.
Wetland	Shrub	The Class Scrub-Shrub Wetland includes areas dominated by woody vegetation <6 m (20 ft) tall. The species include true shrubs, young trees, and trees or shrubs that are small or stunted because of environmental conditions. All water regimes except subtidal are included.
Wetland	Emergent	The Emergent Wetland Class is characterized by erect, rooted, herbaceous hydrophytes, excluding mosses and lichens. This vegetation is present for most of the growing season in most years. These wetlands are usually dominated by perennial plants. All water regimes are included except subtidal and irregularly exposed.
Wetland	Pond/Lake	UB: The Class Unconsolidated Bottom includes all wetland and deepwater habitats with at least 25 % cover of particles smaller than stones, and a vegetative cover <30 %. Water regimes are restricted to subtidal, permanently flooded, intermittently exposed, and semipermanently flooded. AB: The Class Aquatic Bed includes wetlands and deepwater habitats dominated by plants that grow principally on or below the surface of the water for most of the growing season in most years. Water regimes include subtidal, irregularly exposed, regularly flooded, permanently flooded, intermittently exposed, semipermanently flooded, and seasonally flooded. L: The Lacustrine System includes wetlands and deepwater habitats with all of the following characteristics: (1) situated in a topographic depression or a dammed river channel; (2) lacking trees, shrubs, persistent emergents, emergent mosses or lichens with >30 % areal coverage; and (3) total area exceeds 8 ha (20 acres). Similar wetland and deepwater habitats totaling <8 ha are also included in the Lacustrine System if an active wave-formed or bedrock shoreline feature makes up all or part of the boundary, or if the water depth in the deepest part of the basin exceeds 2 m (6.6 ft) at low water. Lacustrine waters may be tidal or nontidal, but oceanderived salinity is always <0.5 ‰.
Wetland	Estuarine	The Estuarine System consists of deepwater tidal habitats and adjacent tidal wetlands that are usually semi-enclosed by land but have open, partly obstructed, or sporadic access to the open ocean, and in which ocean water is at least occasionally diluted by freshwater runoff from the land. The salinity may be periodically increased above that of the open ocean by evaporation. Along some low-energy coastlines there is appreciable dilution of sea water. Offshore areas with typical estuarine plants and animals, such as red mangroves (*Rhizophora mangle*) and eastern oysters (*Crassostrea virginica*), are also included in the Estuarine System.[3]
Wetland	Riverine	The Riverine System includes all wetlands and deepwater habitats contained within a channel, with two exceptions: (1) wetlands dominated by trees, shrubs, persistent emergents, emergent mosses, or lichens, and (2) habitats with water containing ocean-derived salts in excess of 0.5 ‰. A channel is "an open conduit either naturally or artificially created which periodically or continuously contains moving water, or which forms a connecting link between two bodies of standing water" (Langbein and Iseri 1960:5).
Hydrological Regime	Permanently Flooded	Water covers the land surface throughout the year in all years. Vegetation is composed of obligate hydrophytes.
Hydrological Regime	Temporarily Flooded	Surface water is present throughout the year except in years of extreme drought.
Hydrological Regime	Semipermanently Flooded	Surface water persists throughout the growing season in most years. When surface water is absent, the water table is usually at or very near the land surface.
Hydrological Regime	Seasonally Flooded	Surface water is present for extended periods especially early in the growing season, but is absent by the end of the season in most years. When surface water is absent, the water table is often near the land surface.
Hydrological Regime	Semipermanently Flooded	The substrate is saturated to the surface for extended periods during the growing season, but surface water is seldom present.
Hydrological Regime	Temporarily Flooded	Surface water is present for brief periods during the growing season, but the water table usually lies well below the soil surface for most of the season. Plants that grow both in uplands and wetlands are characteristic of the temporarily flooded regime.
Hydrological Regime	Intermittently Flooded	The substrate is usually exposed, but surface water is present for variable periods without detectable seasonal periodicity. Weeks, months, or even years may intervene between periods of inundation. The dominant plant communities under this regime may change as soil moisture conditions change. Some areas exhibiting this regime do not fall within our definition of wetland because they do not have hydric soils or support hydrophytes.
Hydrological Regime	Artificially Flooded	The amount and duration of flooding is controlled by means of pumps or siphons in combination with dikes or dams. The vegetation growing on these areas cannot be considered a reliable indicator of water regime. Examples of artificially flooded wetlands are some agricultural lands managed under a rice-soybean rotation, and wildlife management areas where forests, crops, or pioneer plants may be flooded or dewatered to attract wetland wildlife. Neither wetlands within or resulting from leakage from man-made impoundments, nor irrigated pasture lands supplied by diversion ditches or artesian wells, are included under this modifier.

Appendix C. Violin plot representing the density (width) of plots in relation to latitude (decimal degrees)



Appendix D. Environmental covariates considered for each species. Cells containing "x" indicate variables that were included in respective species analyses

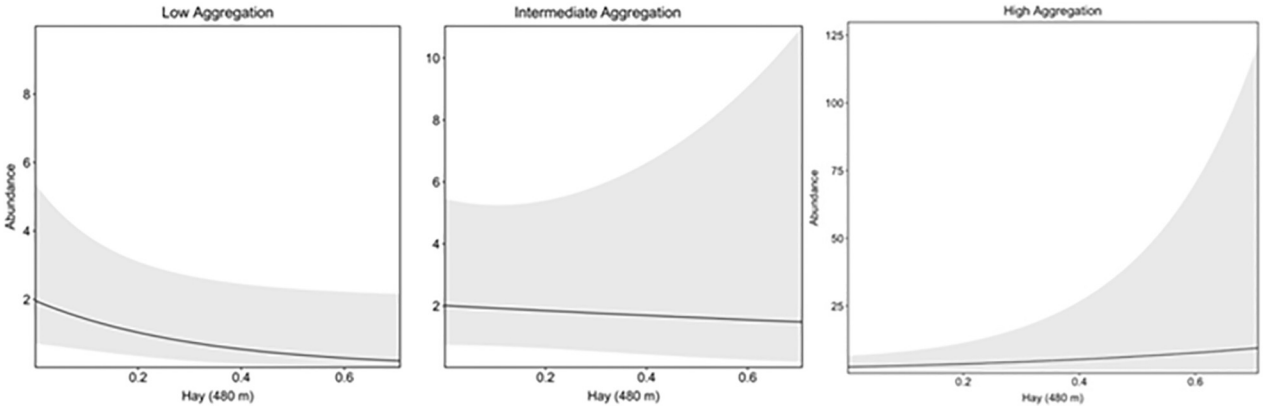
Species	Wetland Amount						Wetland Ephemerality		Wetland Diversity			Land Use			
	All wetlands	Shallow palustrine	Emergent	Shrub	Forest	Pond	All wetlands	Shallow palustrine	All wetlands	Shallow palustrine	Wetland-Regime	Road density	Impervious	Cultivated crops	Hay
Blanding's turtle		x	x	x	x			x		x	x	x	x		
Spotted turtle		x	x	x	x			x		x	x	x	x	x	x
Painted turtle	x		x	x	x	x	x		x			x	x	x	x
Snapping turtle	x		x	x	x	x	x		x			x	x	x	x
Eastern mud turtle	x		x	x	x	x	x		x			x	x	x	x
Striped mud turtle	x		x	x	x	x	x		x			x	x	x	

Appendix E. Summary of information related to individual species models, including total number of sites, error distribution (nb = negative binomial, zip = zero-inflated Poisson), and the maximum number of detection, wetland, and land use covariates considered for each species

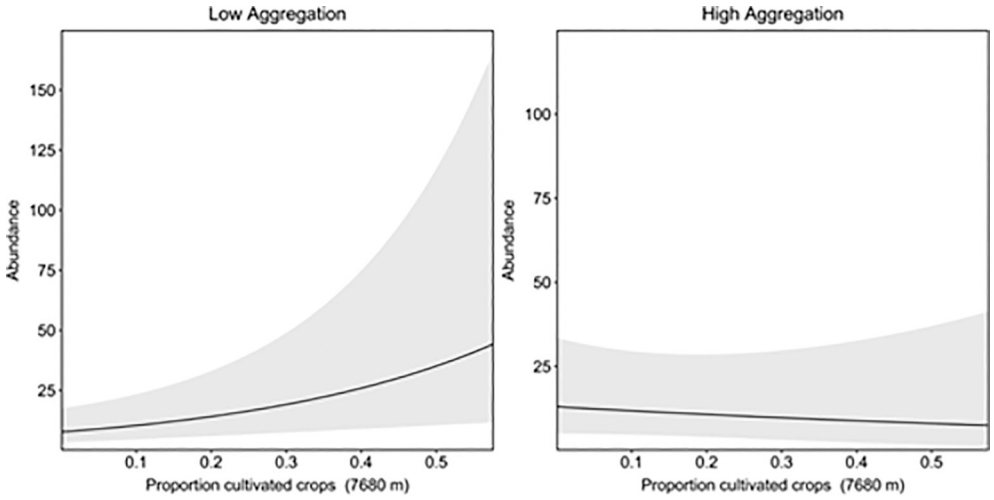
Species	Detections	Sites with detection	Sites sampled	Proportion sites with detection	Max. # detection covariates	Max. # wetland covariates	Max. # land use covariates	Error distribution
Blanding's turtle	77	21	66	0.32	2	1	1	Negative binomial
Spotted turtle	1087	188	522	0.36	4	3	3	Negative binomial
Painted turtle	2328	201	354	0.56	4	3	3	Negative binomial
Snapping turtle	272	143	522	0.27	4	3	3	Zero-inflated Poisson
Eastern mud turtle	662	127	281	0.45	4	3	3	Negative binomial
Striped mud turtle	251	62	200	0.31	2	2	2	Negative binomial
Pond slider	74	21	178	0.12	NA	NA	NA	NA
Eastern musk turtle	163	42	518	0.08	NA	NA	NA	NA
Wood turtle	7				NA	NA	NA	NA
Northern red-bellied cooter	6				NA	NA	NA	NA
Florida softshell	2				NA	NA	NA	NA
Loggerhead musk turtle	1				NA	NA	NA	NA

Appendix F. Plots displaying 95 % confidence intervals associated with interactions between land use and wetland aggregation

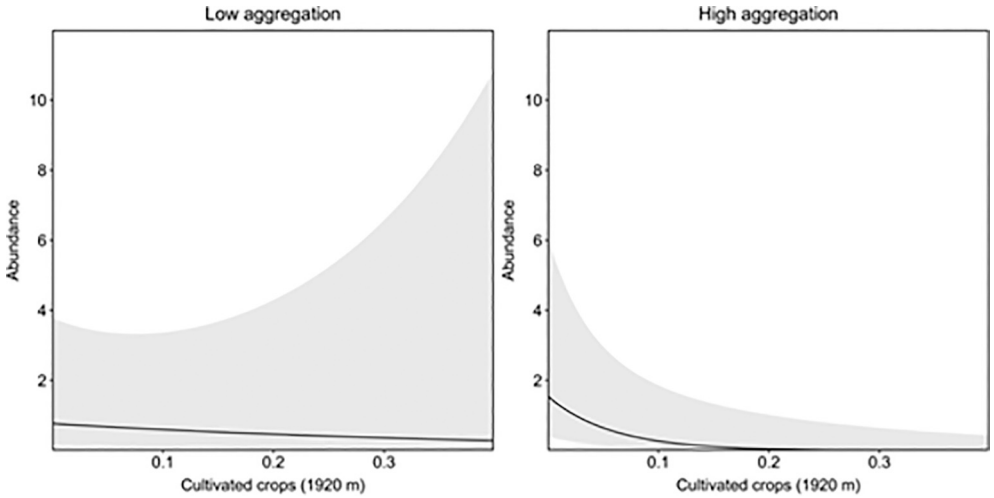
Spotted turtle (*Clemmys guttata*)



Snapping turtle (*Chelydra serpentina*)



Striped mud turtle (*Kinosternon baurii*)



Appendix G. Detection covariates estimates (standard error) for individual species abundance models. All covariates were strong predictors of detection probability within all models

Species		Detection Covariates			
Blanding's turtle	Covariates	Date	$Date^2$		
	Model 1	4.19 1.315	−1.61 0.543		
Spotted turtle	Covariates	GDD	Visit	Water temp	Date
	Model 1	−0.926 (0.153)	−0.218 (0.03)	0.380 (0.074)	−0.775 (0.118)
	Model 2	−0.941 (0.151)	−0.219 (0.03)	0.375 (0.074)	−0.773 (0.117)
	Model 3	−0.93 (0.152)	−0.219 (0.03)	0.378 (0.074)	−0.774 (0.118)
Painted turtle	Covariates	Visit	Water temp	Date	$Date^2$
	Model 1	−0.269 0.0219	0.463 0.0526	−0.561 0.0718	0.143 0.0360
Snapping turtle	Covariates	GDD	Visit	Water temp	$Water\ temp^2$
	Model 1	−0.795 0.1434	−0.280 0.0577	0.789 0.1285	−0.257 0.1020
	Model 1	−0.783 0.1433	−0.280 0.0576	0.793 0.1284	−0.263 0.1022
Eastern mud turtle		GDD	Visit	Water temp	$Water\ temp^2$
		−0.436 0.1622	−0.290 0.0400	0.448 0.0712	−0.134 0.0431
Striped mud turtle	Covariates	Visit	Air temp		
	Model 1	−0.459 0.0712	0.581 0.1757		
	Model 2	−0.456 0.0711	0.551 0.1751		

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