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A Comparison of the Effects of Habitat Type and Human Influence on Occupancy of Freshwater Turtles in the Mississippi Embayment

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ABSTRACT

Freshwater turtles are highly diverse in the southeastern United States, yet few studies document how diversity is distributed in agricultural and rural landscapes. Furthermore, most previous work did not compare distributions between pond and river habitats with potential differences in selective pressures. We surveyed 64 sites in the Mississippi embayment and evaluated how surrounding land use, road density, and habitat type affected species' occupancy with a focus on *Macrochelys temminckii*. We observed that turtles were less likely to occur in locations surrounded by high road density. We observed variation in species' responses to agricultural land-use that partially depended on preferences for lotic habitat. *M. temminckii* were rare and negatively affected by road density and unassociated with agricultural land-use. Variation among species can likely be attributed to differences in species traits, but more studies evaluating land-use effects on species occupying lentic versus lotic habitats could create more effective conservation strategies.

1 | Introduction

Freshwater habitats and species are imperiled throughout the southeastern U.S. (Buhlmann et al. 2009; Strayer and Dudgeon 2010; Elkins et al. 2019). In the Mobile Basin alone, 40% of known freshwater taxa are extirpated, considered species of concern, or threatened and/or endangered at the state or federal level (Lydeard and Mayden 1995). Although many declines of freshwater species can be attributed to habitat loss through manipulation to the water flow (e.g., dams or canals; Poff et al. 2007) or to the land surface itself (e.g., filling in wetlands; Gibbs 2001), other species experience individual and population level-effects from human activities within the watershed (e.g., Steen and Gibbs 2004; Roberts et al. 2021). A large body of research has outlined the important ways that agriculture and urbanization degrade habitat quality including nutrient enrichment, heavy metals, and sedimentation (Smith et al. 1987; Walsh et al. 2005; Scanlon et al. 2007). Ultimately, land-use changes in watersheds alter multiple habitat conditions in ways that can interact to contribute to declining species commonness.

Freshwater turtles are recognized as the most threatened vertebrate taxa (Lovich et al. 2018). However, the anthropogenic and environmental drivers of their distributions and status in the southeast are still largely unknown. Freshwater turtle

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Summary

Practitioner Points

- Pond and river turtles exhibit similar patterns in responses to land-use and human influence.
- Turtles can persist in agricultural landscapes, but more work is needed about their long-term success.

populations are sensitive to stressors within their environment due to a suite of life history traits (e.g., delayed sexual maturity, long lifespans, and low recruitment potential), thus making population recovery and conservation challenging (Congdon et al. 1994; Ernst and Lovich 2009). However, considerable life-history variation exists (e.g., diet, basking, terrestrial dispersal, body size, and reproduction behaviors) among turtle species, and their sensitivity to the different stressors depends upon these other traits. For example, some may be most threatened by road mortality during terrestrial breeding and overwintering migrations, while other large species may be most threatened by commercial harvest or habitat modifications (Kenneth Dodd 1990; Bennett et al. 2010; Mali et al. 2014). Compounding this natural history variation is that several species can inhabit rivers, ponds, lakes, and wetlands with very different environmental properties and selective pressures (Ernst and Lovich 2009). Therefore, it is unsurprising that studies characterizing distributions of freshwater turtles often fail to identify key characteristics or properties of watersheds that are more likely to support high turtle diversity at the landscape scale (e.g., Rizkalla and Swihart 2006; Stokeld et al. 2014; Fyson et al. 2020, but see Guzy et al. 2013; Roberts et al. 2023).

Several landscape-scale factors contribute to the decline of freshwater turtles, including road density and associated terrestrial habitat fragmentation (Steen and Gibbs 2004; Guzy et al. 2013; but see Paterson et al. 2021; Buchanan et al. 2019). Notably, agriculture and urbanization are rarely linked to turtle occupancy and abundance, but previous studies largely occurred within lentic habitat and not lotic (Rizkalla and Swihart 2006; Guzy et al. 2013; Stokeld et al. 2014; Fyson et al. 2020). As an inherently connected landscape feature, turtle distributions in rivers may not be subject to the same drivers as isolated ponds and lakes (e.g., Roberts et al. 2023). Furthermore, changes in their watersheds may affect rivers and ponds differently. For example, erosion may fill in a pond to make it shallower or more turbid, reducing primary production and potentially reducing the food available to turtles (Madsen et al. 2001; Oertli and Parris 2019). In a river, erosion may increase turbidity as well as fill in the spaces between refuges, making it more challenging for turtles to evade high flows, bask, and consume enough resources (Allan 2004; Gregory 2006; Adkins Giese et al. 2012; Schaffer et al. 2016), which can all be exacerbated by channelization and other channel manipulations (Lenhart et al. 2013; Hartson et al. 2014). Changes in terrestrial landscapes that contribute to flow regime variation may have a strong effect on turtles inhabiting rivers while having little effect on those inhabiting ponds and lakes (Reese and Welsh 1998; Bennett et al. 2010). More research is needed to assess whether habitat type, such as lentic versus lotic, is a strong contributing factor in determining the success of turtles in the human-modified landscapes of the rural southeastern United States.

The southeastern United States has 44 species of freshwater turtles, making it a global hotspot for turtle diversity (Buhlmann et al. 2009; Ennen et al. 2017, 2020). Significant variation exists among turtles that inhabit the region with turtles ranging in carapace size from 10 cm (e.g., *Sternotherus odoratus*) to over 1 m in length (*Macrochelys temminckii)* and in terrestrial and aquatic habitat use and needs (Ernst and Lovich 2009; Xiao et al. 2023). For example, *M. temminckii* is closely associated with large rivers and their oxbows lakes and backwaters while *Trachemys scripta* is a regular occupant of small farm ponds as well as rivers and larger lakes (Ernst and Lovich 2009). This study was initiated to evaluate the distribution of *M. temminckii* in Tennessee as its status is considered for increased federal protection (Garig et al. 2021). As a formerly harvested species with delayed sexual maturity, their populations have been documented as in decline throughout their range, and their range has shrunk as new genetic evidence elevated previously undescribed lineages to species (Adkins Giese et al. 2012; Thomas et al. 2014). However, *M. temminckii* are regularly captured alongside a range of other southeastern species allowing for comparisons to be made among species. Our objective was to assess how aquatic habitat use interacted with surrounding land-use and road density to affect freshwater turtle occupancy in the Mississippi embayment.

2 | Materials and Methods

2.1 | Study Context

We evaluated turtle occupancy within the 21-county region in the Mississippi embayment of western Tennessee (Figure 1; Garig et al. 2021). All sites were located along the floodplain of the Mississippi River or in major drainages including the Wolf, Hatchie, Forked Deer, and Obion watersheds. Lotic sites were characterized by slow-moving, meandering rivers that frequently flood (Dodd and Whiles 2019). Lentic sites were more variable and included oxbow lakes, swamps, sloughs, and backwater areas (Dodd and Whiles 2019). Historically, rivers were channelized, wetlands were drained and ditched, and bottomland forests were cleared for agriculture in this area. Forests adjacent to these sites are characterized as either cypress-tupelo forests including bald cypress (*Taxodium distichum*) and water tupelo (*Nyssa aquatica*) or bottomland hardwood forests characterized by swamp chestnut oak (*Quercus michauxii*) and water oak (*Quercus nigra*). In this area, alluvial soils are highly conducive for agriculture, which is the dominant land-cover type. Cotton, corn, wheat, sorghum, and soybeans are produced on an industrial scale in the region. Memphis is the primary urban area containing 60% of the population in this region. Therefore, agriculture remains the most significant change in the terrestrial landscape. Within a 1 km buffer of our sites, urban development and forest cover ranged from 0% to 25% of the buffer while agriculture covered 29 ± 4% of the buffer with up to 85% of some buffers being used for agriculture.

2.2 | Field Methods

We surveyed 64 sites once during April through October from 2016 to 2018. Each survey included ten traps deployed for three

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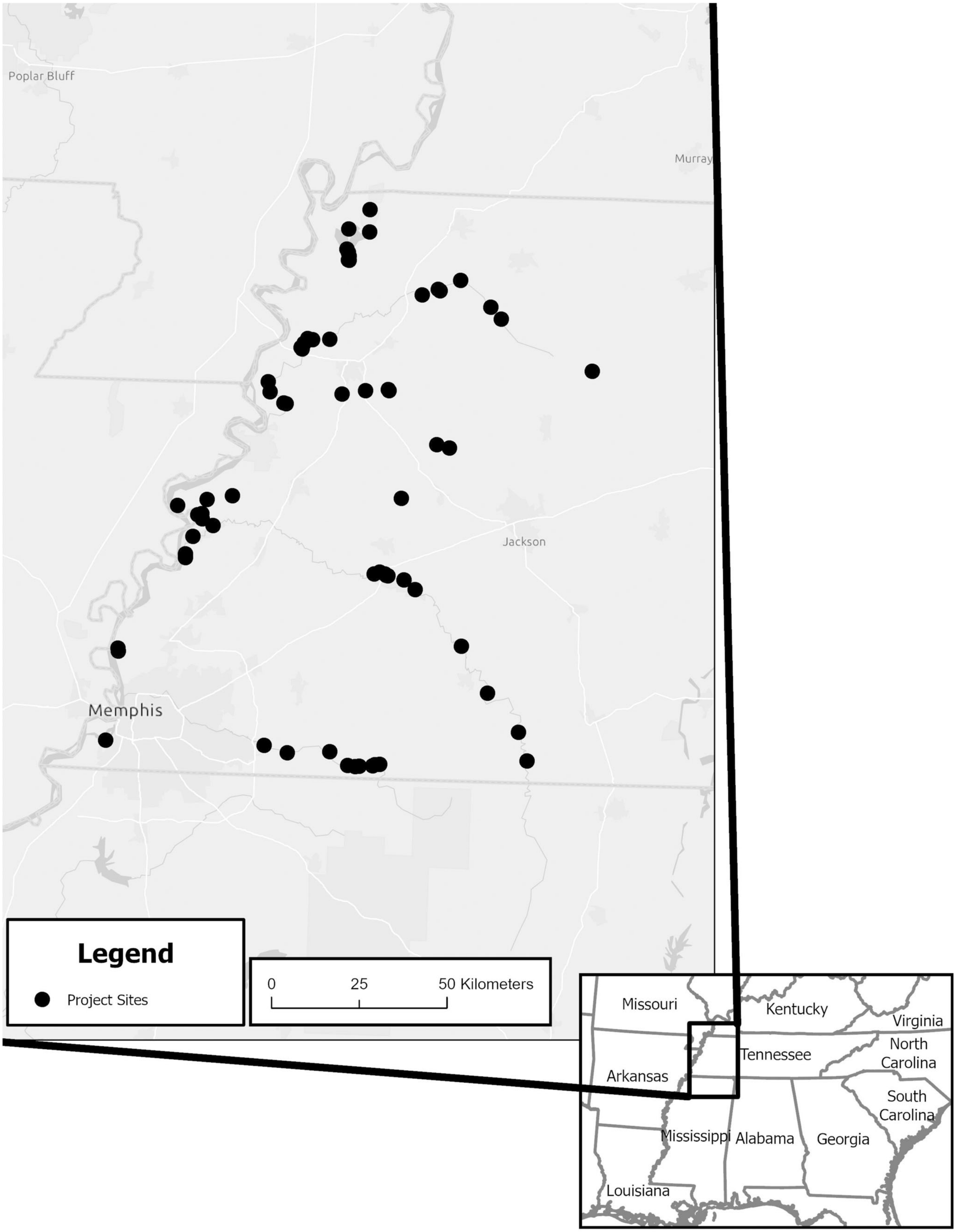

FIGURE 1 | Map illustrating sample sites in the Mississippi River embayment of Tennessee. Sites represented the Wolf, Hatchie, Forked Deer, and Obion watersheds.

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consecutive trap nights within a season. Sites were not resurveyed across years. We used hoop net traps (flat throats) baited with various species of local fish. All traps were re-baited daily and set near structures or submerged vegetation. Traps were set with buoys and at a depth that would allow entrapped turtles to surface for air while maintaining the throat of the trap in the water. More details about the trapping protocols and details about the traps may be found in Ennen et al. (2021) that documented widely overlapping detection probabilities for the species observed in this study. Although this was a rapid assessment, we used a diversity of trap types to maximize detection of the range of species observed within this community (Ennen et al. 2021). This prior study also evaluated similarities between detection probability and catch-per-unit-effort, which revealed similar patterns among trap type suggesting that trapping biases were likely overcome by using different trap types. Thus, differences in detection and occupancy reflect variation in the commonness of each species at each site and in the region. Upon capture, turtles were identified to species and released at their point of capture.

2.3 | Spatial Analyses

To assess the spatial factors for these 64 sites, Environmental Science Research Institute (ESRI) ArcMap software was used to create 2 km buffers around each sample site. This buffer size was selected to reflect the dispersal abilities of all turtles in this study (e.g., Steen and Gibbs 2004). The National Land Cover Data set (Dewitz and US Geological Survey 2021) was obtained from 2016 and the ESRIs Reclassify tool to simplify the data into the following categories: Water (NLCD Values: 11), Developed (NLCD Values: 21,22,23,24), Barren Land (NLCD Values: 31), Forests (NLCD Values: 41,42,43), Shrubs (NLCD Values: 52), Grasslands (NLCD Values: 71), Agriculture (NLCD Values: 81,82), and Wetlands (NLCD Values (90,95). The reclassified layer was clipped using the 2 km buffers for each sample site. Using the "Count" column in the raster attribute table for each buffered site, the percent coverage was calculated for each category. To create an "Undisturbed" value, the percentages from the Water, Barren Land, Forests, Shrubs, Grasslands, and Wetlands were added together.

Additionally, Road Density was determined for each buffered site. TIGER/Line Shapefiles (TIGER 2019) were downloaded for each county within the study area. These lines were then combined with the buffers using the Intersect tool within ArcMap. Each road line was recalculated into meters and exported. The total road lengths were summarized for each buffered area and divided by the total area of the buffer to get a road density value.

2.4 | Statistical Analyses

We conducted a multi-species occupancy model to evaluate the effects of landcover and aquatic habitat type on occupancy. In addition to occupancy and species-level responses to covariates, multispecies models allow for the estimation of species richness and community-level responses to site characteristics while accounting for imperfect detection (Kéry and Royle 2015; Gould and Peterman 2021; Ennen et al. 2021). We acknowledge that this approach is limited in its ability to detect nuanced or subtle changes because it is designed to document the most extreme responses to change—local extirpation, but this reflects the most commonly used landscape-scale response metric in turtles (e.g., Buchanan et al. 2019; Roberts et al. 2023, but see Rosenbaum et al. 2023). To account for landcover effects on occupancy, we evaluated landcover within a 1 km radius around site centroids. To reduce effects of collinearity between cover types, we conducted a principal components analysis (PCA), including percent cover of agriculture, forest, wetland, undisturbed, developed land, and road density (km^2). We then retained principal components with eigenvalues greater than one, to be included as covariates in the occupancy model. We ultimately included two components from the landcover PCA. In addition to landcover, we classified each site as either lentic or lotic, and included a binary variable indicating that a site was lentic within the model.

To estimate the effects of landcover components and lentic site condition on trap-occupancy $z_{i,k}$ at trap i within site s, we modeled:

$$Z_{i,k} \sim \text{bernoulli}(\psi_{i,k}),$$

$$\text{logit}(\psi_{i,k)} = \text{lpsi}_k + \text{beta.PC1}_k \times \text{PC1}_i + \text{beta.PC2}_k \times \text{PC2}_i + \text{beta.Lentic}_k \times \text{Lentic},$$

where all beta terms were species-specific and lpsi was a random intercept for each species. We then averaged across traps to estimate site-level occupancy.

Additionally, we estimated detection following the same methods outlined in Ennen et al. (2021), where detection probability $p_{i,j,k}$ of species k in trap i on visit j is modeled:

$$y_{i,j,k} \sim \text{Binomial}(z_{i,k} \times p_{i,k}),$$

$$\text{logit}(p_{i,k}) = \text{lp}_k + \text{alpha1}_k \times \text{trap2}_i + \text{alpha2}_k \times \text{trap3}_i,$$

where all alpha parameters were species-specific and trap type one was the reference level. All alpha and beta parameters were estimated via non-informative priors, normally distributed around hyper-parameters for both the mean and precision. The hyper-parameter means were normally distributed on zero, with a precision of 0.1. The hyper-parameter precisions were uniformly distributed between the interval [0,2]. The intercepts for detection and occupancy were drawn from a multivariate normal distribution, with a log-normally distributed mean and inverse-Wishart distributed precision (Kéry and Royle 2015).

In addition to species-specific estimates of the effects of covariates, we derived site-level species richness (alpha diversity). We ran the model for a total of 105,000 iterations across three chains, with a burn-in of 5000 and a thinning rate of 10, saving 10,000 samples per chain, yielding a posterior sample of 30,000. We evaluated model fit by visually inspecting chain

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convergence, ensuring all parameters had Gelman-Rubin fit statistic values (< 1.1). Additionally, we evaluated model predictive ability using a Freeman-Tukey diagnostic by comparing observed data to estimates from the model, generating a Bayesian *p*-value (BP). Models with BP values that approach 0.5 are considered to have high predictive ability.

3 | Results

Across all surveys, we detected 11 species of turtles (*Apalone spinifera, A. mutica, Chelydra serpentina, Chrysemys dorsalis, Graptemys pseudogeographica, G. ouachitensis, Kinosternon subrubrum, M. temminckii, Pseudomys concinna, S. odoratus*, and *T. scripta*), totaling 3026 observations over a 3 year period. We removed two species (*A. mutica* and *G. ouachitensis*) found at only one site each, and we modeled the remaining nine species. Across all sites, we detected a maximum of seven species and a minimum of zero, and on average detected between two and three species per site (Table 1). Species richness across all sites averaged four species per site (3–5). Between basins, sites sampled within the Forked Deer River basin had the highest alpha diversity (4.73, 3.71–5.86) and had significantly higher diversity than sites located in the Hatchie River basin (3.50, 2.54–4.62). Species richness among all other basins were not significantly different (Table 1). Of the species included in the model, the most observed species was *T. scripta*, which was detected at least once at 57 sites while *K. subrubrum* was detected at only two sites. Mean species detection varied between 2% and 55%, suggesting considerably different sampling efficacy for different species (Table 2).

Our PCA results indicated that two components had eigenvalues greater than 1, accounting for 47% and 33% of variance, respectively. Component one (PC1) was negatively correlated with agriculture (−0.99) and positively related to undisturbed (0.98) and wetland (0.81) land cover (Figure 2). Component two (PC2) was negatively correlated with road density (−0.84), developed land (−0.82), and to a lesser extent forest cover (−0.63) and did not exhibit significant positive correlation with any land cover (Figure 2). All other components represented ~20% of variance and were not included in the occupancy model.

Our occupancy model indicated mean site occupancy ranging from 9% to 89%, depending on the species (Table 2). For the most widely distributed species, *T. scripta* and *C. serpentina*, mean site occupancy was 89% and 86%, respectively (Table 2).

TABLE 1 | Turtle species richness observed in surveys of five river basins in the Mississippi River embayment of Tennessee. Mean and 95% credible intervals for species richness are reported. The column *n* indicates the number of surveyed sites within each basin.

	n	Mean	2.50%	97.50%
Forked Deer	7	4.73	3.71	5.86
Hatchie	13	3.51	2.54	4.62
Mississippi	9	3.83	2.78	5.22
Obion	26	4.25	3.15	5.42
Wolf	9	4.15	3.22	5.22

Two species, *K. subrubrum* and *M. temminckii*, were considerably less widespread and were predicted to occur at 25% and 9% of sites, respectively (Table 2). All other species were predicted to occur at between 34% and 51% of visited sites, on average (Table 2).

Overall, site occupancy was lower in sites with higher PC1 scores ($\beta = -0.61$, 89% HDI = −0.91 to −0.28), indicating higher occupancy in sites surrounded by agriculture than those with higher undisturbed or wetland cover type. Although effect sizes for specific responses varied, two species exhibited significant negative responses to PC1 (*A. spinifera* and *G. pseudogeographica*), and all species mean responses were negative (Figure 3A). There was less consensus in observed responses to PC2 (Figure 3B; $\beta = 0.17$, 89% HDI = −0.12 to 0.46). Although all species exhibited nonsignificant responses, both *T. scripta* and *G. pseudogeographica* exhibited some evidence for positive response, indicating a weak preference for less developed or less forested land (Figure 3B).

Overall, occupancy of all species was not significantly higher in lentic habitat ($\beta = 0.26$, −0.46 to 0.93), however, three species had > 80% probability that occupancy was higher in lentic habitat (Figure 4). Of these, *C. serpentina, T. scripta*, and *C. dorsalis* exhibited the greatest likelihood of higher occupancy in lentic habitat (Figure 4; listed in order of magnitude of preference). Three species, *P. concinna, A. spinifera*, and *G. pseudogeographica* indicated marginal preferences for lotic habitat and were more likely to occur in lotic sites (Figure 4). Habitat type had an intermediate effect relative to the two PCA axes described above. PC1 was 2.34 times more important than habitat type, which was 1.53 times more important than PC2 in describing turtle occupancy.

4 | Discussion

The Mississippi embayment in western Tennessee has a heterogeneous mix of habitats ranging from large rivers to oxbow lakes and flooded forests for which some species exhibit higher habitat specificity than others. Aquatic habitat characterization indicated that some species appear to specialize while others remain generalists. Although most studies identify road density as a common and consistent predictor of population success (Gibbs and Shriver 2002; Fahrig and Rytwinski 2009), our study observed mixed responses to road density with most showing either no response or a weak negative response to road density. Although this study did not include highly urban areas with high road densities, it does survey the rural land-use that covers far greater area for which other components of anthropogenic change may be more important in limiting turtle occupancy (e.g., Jackson et al. 2022). In this rural landscape, agricultural land-use was a more important predictor with species-specific relationships. Nearly all species' occupancy was positively associated with agricultural habitat disturbance while *M. temminckii* showed no relationship with agricultural development.

Agricultural land-use affects terrestrial conditions surrounding ponds that can have consequences for aquatic habitat conditions, but it remains unclear to what degree the impacts of changing land-use affect different segments of the population.

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TABLE 2 | Estimated site-level occupancy and detection probabilities for all turtle species captured in surveys of the Mississippi River embayment of Tennessee in sufficient numbers for occupancy modeling.

	Site occupancy probability			Detection probability		
Species	Mean	2.50%	97.50%	Mean	2.50%	97.50%
Apalone spinifera	0.51	0.45	0.56	0.46	0.36	0.56
Chelydra serpentina	0.86	0.83	0.89	0.64	0.57	0.70
Chrysemys dorsalis	0.38	0.09	0.67	0.14	0.02	0.26
Graptemys pseudogreographica	0.38	0.33	0.44	0.44	0.33	0.55
Kinosternon subrubrum	0.25	0.03	0.58	0.11	0.00	0.23
Macrochelys temminikii	0.09	0.05	0.16	0.39	0.09	0.68
Pseudemys concinna	0.34	0.19	0.48	0.23	0.10	0.35
Sternotherus oderatus	0.36	0.23	0.47	0.36	0.21	0.51
Trachemys scripta	0.89	0.89	0.89	0.91	0.88	0.95

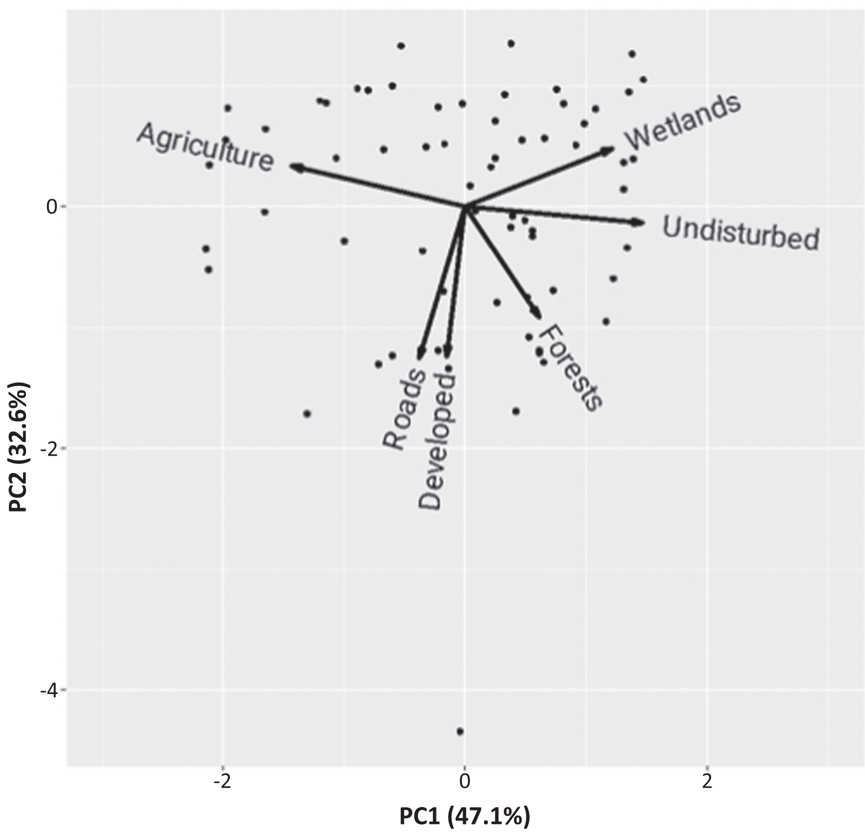

FIGURE 2 | Results of a principal components analysis of our potential predictor variables. The dominant axis primarily describes differences between sites surrounded by agriculture or by forest. The secondary axis primarily described the effects of road mortality and human development. PC1 represented 47.1% of the variation with PC2 representing 32.6% of the variation.

For example, forest clearing and soil management could attract female turtles seeking nesting habitat, but mechanized management of crops can also cause injury to females or other turtles dispersing among habitats (Beaudry et al. 2010; Saumure et al. 2007; McCluskey et al. 2022). Changes in nest temperatures in agricultural fields could affect sex ratios of hatchlings or warmer water and higher concentrations of nutrients in habitats adjacent to agricultural fields could contribute to higher metabolism and growth (Freedberg et al. 2011; Haskins and Tuberville 2022). Similar to other studies in heavily human modified landscapes, the presences of ponds regardless of their surrounding land use like agriculture or golf courses may be beneficial for maintaining landscape occupancy of turtles (Failey et al. 2007; Roberts et al. 2023). Ponds on golf courses or in agricultural landscapes are characterized by intense forest clearing, providing significantly less dense canopy cover. Lower canopy cover in these areas could allow greater basking and nesting opportunities. However, without concomitant population information, it is unclear if turtles are simply surviving or thriving in these ponds, which is a well-understood critique of

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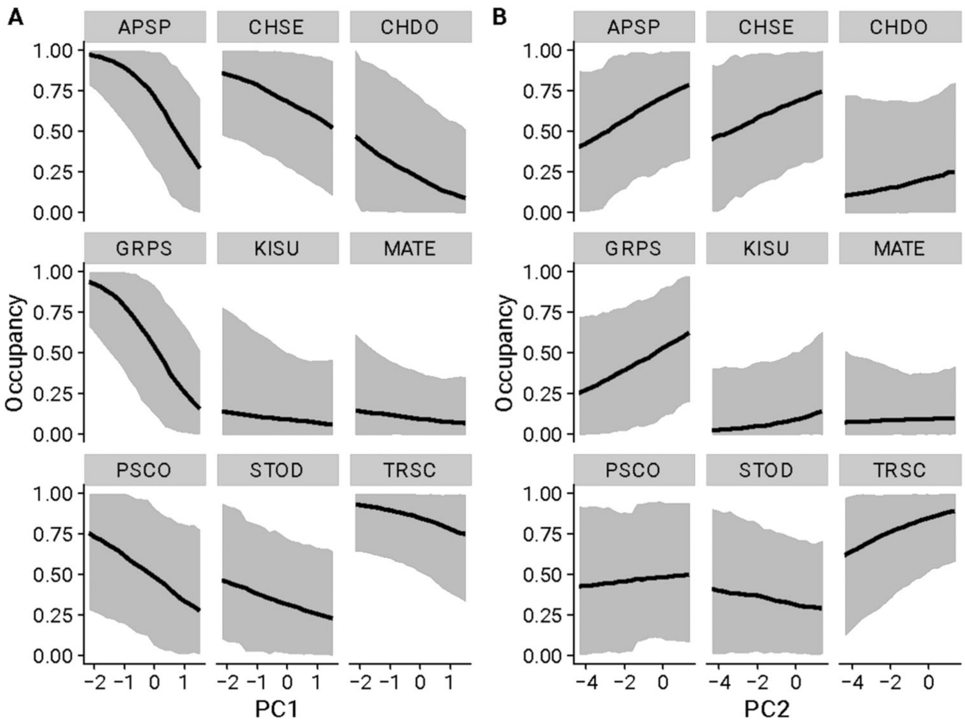

FIGURE 3 | Predicted responses of species occupancy probability to changes along the principal components axes. The dark black line represents the mean predicted response and the gray lines represent the 95% credible interval for the relationship. Negative relationships with PCI (A) indicate associations with agricultural surroundings versus undisturbed and forested land cover. Positive relationships with PC2 (B) indicates higher occupancy in landscapes with fewer roads and less developed landscapes. Species abbreviations are as follows: APSP, *Apalone spinifera;* CHDO, *Chrysemys dorsalis;* CHSE, *Chelydra serpentina;* GRPS, *Graptemys pseudogeographica;* KISU, *Kinosternon subrubrum;* MATE, *Macrochelys temminckii;* PSCO, *Pseudemys concinna;* STOD, *Sternotherus odoratus;* TRSC, *Trachemys scripta*.

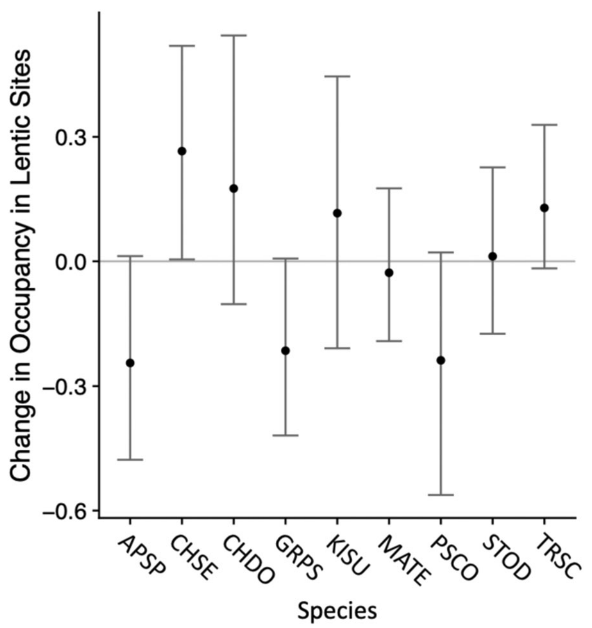

FIGURE 4 | Estimates of the mean effect of lentic habitat (±95% credible intervals) on the site occupancy of freshwater turtles in the Mississippi embayment. The line at 0.0 indicates predictions that habitat type does not affect species occupancy. Species abbreviations are as follows: APSP, *Apalone spinifera;* CHDO, *Chrysemys dorsalis;* CHSE, *Chelydra serpentina;* GRPS, *Graptemys pseudogeographica;* KISU, *Kinosternon subrubrum;* MATE, *Macrochelys temminckii;* PSCO, *Pseudemys concinna;* STOD, *Sternotherus odoratus;* TRSC, *Trachemys scripta*.

occupancy-level studies like ours. Although alteration to the thermal, nutrient, and sediment regimes of rivers is known to disrupt riverine food webs and the success of a number of riverine taxa (e.g., Dodd et al. 1988; Schürings et al. 2022), agriculture in this study had a positive effect on riverine turtles similar to another study that found positive effects on cosmopolitan species (Sterrett et al. 2011). *Apalone spinifera* often uses sandy and silty channel features for basking and nesting, which may be more common in agricultural landscapes (Gibbs et al. 2007) and many river turtles are rarely terrestrial (Ward and Jackson 2008; Ernst and Lovich 2009).

There are many potential ramifications for the positive correlation between turtle occupancy and agricultural land use. Ponds in developed areas, such as golf courses and agriculture, are often found to be important habitats for freshwater turtles (Winchell and Gibbs 2016; Tu and Trulio 2022). In agricultural landscapes where many natural ponds have been filled or drained and rivers have been channelized, practitioners should not discount the value of an agricultural site for preserving landscape distributions of freshwater turtles. The use of cattle to maintain agricultural aquatic habitats has also been found to be beneficial for two species of turtles (Geluso et al. 2020; Tesauro and Ehrenfeld 2007). Prescribed grazing could be used as a mechanism to control invasive species growth and encourage endemic herbaceous growth, but trampling by cattle remains a concern for turtle success (summarized in Riensche et al. 2019). Pesticides, herbicides, and fertilizers that might be applied to commercial agricultural fields could also inhibit embryo

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development of freshwater turtle eggs (de Solla et al. 2011) and growth rates (Willingham 2001), and guidelines for safe use of pesticides, herbicides, and fertilizers around agricultural ponds should be developed to protect turtle populations. Likewise, endemic or rare turtles could potentially benefit from protected riparian zones in otherwise agriculturally-dominated landscapes (e.g., *G. barbouri*, Sterrett et al. 2011).

We observed that some species in this region are cosmopolitan and occupy a wide range of macro-habitat types while others appear to specialize on lentic or lotic habitats. Previous studies have found that freshwater turtles may exhibit habitat partitioning but that there is poor understanding of the factors that drive this partitioning. Ecomorphological matching or diet overlap could be mechanisms by which partitioning is maintained (e.g., Luiselli 2008; Xiao et al. 2023). Although our analysis is not definitive, we recommend more work to identify the ecological interactions that maintain these distribution differences at a landscape scale. For species like *A. spinifera* with more carnivorous diets, riverine habitat may provide better access to fish or large invertebrates than ponds or lakes where species with higher degrees of omnivory or herbivory may perform better. Other studies have also documented habitat partitioning in lakes and ponds and determined that species like *C. serpentina* also appear to be habitat generalists at that scale as well (Anthonysamy et al. 2014). Finally, our results indicate that riverine species and pond species do not differ significantly in responses to anthropogenic change. The three species that occupy rivers at higher rates—*A. spinifera, G. pseudogeographica*, and *P. concinna*—tended to have similar responses to environmental variables as pond species, including *C. spinifera, T. scripta*, and *S. odoratus*.

These surveys document that *M. temminckii* is rare in western Tennessee. Only 22 individuals were captured from four sites (6%), and their estimated occupancy probability was 12 times lower than for the closely related *C. serpentina* and 3.4–12.0 times lower than for all other species evaluated in this study. We could not detect any individuals in the Hatchie or Forked Deer drainages. Of the 11 sampled reintroduction sites, we only detected *M. temminckii* from one site, but genetic analyses suggest that these individuals represented both introduced individuals from Louisiana and native individuals (Garig et al. 2021). Like all species detected in this study, occupancy of *M. temminckii* was negatively associated with urbanization and increased road densities. Despite being one of the most aquatic freshwater turtles in the southeast, females still must find terrestrial nesting habitat, and road mortality may contribute to other stressors limiting the success of *M. temminckii* populations (e.g., Carr et al. 2023; Rosenbaum et al. 2023). However, high road mortality goes hand in hand with human interactions including activities like recreational fishing and the presence of human-subsidized predators (e.g., Murphy et al. 2022; Shook et al. 2023). Agriculture also does not appear to be a strong driver of occupancy patterns of *M. temminckii*, but limited spatial distributions of captures restricts our ability to draw strong inferences about the importance of agricultural land use in the watersheds where *M. temminckii* are found.

Although road mortality is a clear threat to individual freshwater turtles (Ashley and Robinson 1996; Haxton 2000), our study suggests that agricultural land-use could contribute to shifts in species composition and interact with other stressors in a rural and agricultural landscape. Furthermore, more research is needed to understand the traits that contribute to habitat specialization in freshwater turtles and to describe the effects that different threats may have relative to the habitat type that is being affected. Despite having moderate detection probabilities, *M. temminckii* appears to be rare in western Tennessee, and conservation efforts need to be identified for the sites where they remain (Howey and Dinkelacker 2013). There is mixed evidence to suggest that minimizing road mortality could contribute to improving the population status, while some evidence suggests historical harvest as a key reason for rarity. The long lifespans of *M. temminckii* suggest that short-term actions are likely to be ineffective without long-term planning.

Author Contributions

Rowland Fournier: writing – original draft (equal), writing – review and editing (equal). **Joshua R. Ennen:** conceptualization (equal), data curation (equal), funding acquisition (equal), investigation (equal), methodology (equal), supervision (equal), writing – review and editing (equal). **Philip R. Gould:** formal analysis (equal), visualization (equal), writing – review and editing (equal). **Kristen K. Cecala:** supervision (equal), writing – original draft (equal), writing – review and editing (equal). **Sarah Sweat:** data curation (equal), formal analysis (equal), methodology (equal), validation (equal), writing – review and editing (equal). **Dustin Garig:** data curation (equal), investigation (equal), methodology (equal). **Robert Colvin:** investigation (equal), resources (equal). **Jon M. Davenport:** conceptualization (equal), data curation (equal), funding acquisition (equal), investigation (equal), project administration (equal), writing – review and editing (equal).

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Ethics Statement

All work was conducted under appropriate permits from the Tennessee Wildlife Resources Agency (TWRA 1787) and Institutional Animal Care and Use Committees at the Tennessee Aquarium and Southeast Missouri State University (TNAQ 16-02; SEMO 012015-01).

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The corresponding author will provide data for any reasonable request.

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