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Effect of Environmental Change on the Trait Composition of Fish Communities in the Tennessee River Basin over the Past 20 Years

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Abstract

This study presents a comprehensive analysis of temporal trends in fish communities within the Tennessee River Basin (TnRB), focusing on the intricate interplay between environmental changes and specific species traits. Over two decades of data from the Tennessee Valley Authority's fish biomonitoring program were utilized to investigate how diverse fish communities respond to anthropogenic stressors. Six key morphological and ecological traits, hypothesized to be responsive to environmental changes, were examined across 348 sites within the TnRB. The results reveal substantial spatial heterogeneity in the temporal trends of fish traits, with significant variations observed across subbasins. While overall trends for the entire basin were not statistically significant, subbasin-level analyses unveiled noteworthy changes in temperature affinity, aspect ratio, age at maturity, trophic position, fecundity, and egg size. These findings underscore the dynamic nature of fish communities within the TnRB. The study highlights the importance of considering life history strategies in the context of environmental change, as demonstrated by the consistent decrease in age at maturity across several subbasins. The results also emphasize the need for integrated and adaptive management strategies to conserve the diverse fish communities of the TnRB. By shedding light on the complex relationships between temporal trends in fish traits and their underlying environmental drivers, this research contributes valuable insights for the sustainable management and conservation of this ecologically significant freshwater ecosystem.

Introduction

Freshwater ecosystems have been experiencing increasing water temperatures and alteration of flow regimes due to climatic, river fragmentation, and land use changes worldwide (Capon et al., 2021; Foley et al., 2005; Döll et al., 2010). Impacts on freshwater ecosystems are expected to drive the reorganization of freshwater communities through different mechanisms. Rapid urbanization, agricultural expansion, and industrial development have led to shifts in hydrology, water quality, and habitat availability, potentially reshaping the conditions that freshwater species rely upon for survival and reproduction (Zhu et al., 2014; Tsegaye et al., 2006; Wilkinson et al., 2018).

Concurrently, climate variability and change can influence fish physiology, behavior, and habitat suitability, thereby exerting cascading effects on community structure (Comte et al., 2012; Day et al., 2018). Specifically, the importance of dispersal ability has forced species' distributions to higher elevations, reduced habitat suitability in tributaries, and made smaller-bodied fish more vulnerable (Troia & Giam, 2019; Troia et al., 2019). Anthropogenic influences, ranging from dam construction to land use change, have also had significant impacts. Dams interrupt the pathways of migratory fish (Barbarossa et al., 2020), and urbanization and deforestation create unstable environments that favor opportunistic strategists that reproduce quicker (Winemiller et. al., 1992). Alterations in flow regimes, sediment transport, and nutrient loading have transformed the physical and chemical attributes of aquatic environments, potentially favoring certain taxa while detrimentally affecting others (Zhu et al., 2014; Comte et al., 2021).

Understanding how fish communities respond to environmental changes through specific traits is crucial, as demonstrated by previous research on how life history traits modify community responses to flow alteration (Mims et al., 2010; Rodriguez-Dominguez et al., 2022). Rising temperatures may favor certain life history traits, such as lower fecundity and age at maturity, encouraging the dominance of opportunistic species adapted to unstable environments (Troia & Giam, 2019; Troia et al., 2019). Examining freshwater biodiversity trends using a trait-based approach allows for the identification of species and communities that remain stable, offering insights into effective management practices to mitigate ongoing and future anthropic impacts on freshwater biodiversity (Capon et al., 2021; Mims & Olden, 2012). The mediation of species responses by specific traits underscores the importance of investigating which combinations of traits make certain species more vulnerable to anthropic stressors, enabling the identification of stable fish communities for targeted conservation and management efforts in the near-term future, particularly in freshwater ecosystems (Keck et al., 2014; Mims et al., 2010; Rodriguez-Dominguez et al., 2022).

Despite freshwater ecosystems harboring a rich diversity of biological organisms—12% of known species on only 0.8% of the world's surface (Abramovitz et al., 1996; Dudgeon et al., 2006), there is limited understanding of how freshwater species and communities are responding and rearranging anthropic impacts over time (Comte et al., 2020). Environmental changes often involve a complex interplay of multiple stressors (e.g., land use, climate change, pollution). Understanding the synergistic or antagonistic effects of these stressors on fish communities requires gathering and analyzing data spanning multiple decades, which is crucial for accurately assessing and quantifying trends and changes. The availability of comprehensive, long-term data sets covering various aspects of the fish communities (species composition, abundance, distribution, etc.) is limited compared to other realms and taxa (Dornelas et al., 2018).

The Tennessee River Basin (TnRB), encompassing a diverse array of aquatic habitats spanning across seven U.S. states, represents a critical component of North America's freshwater biodiversity. Its rivers, streams, and reservoirs serve as vital arteries supporting a rich tapestry of aquatic life, including over 240 fish and 100 mussel species (USGS NAWQA Tennessee River Basin, n.d.). Over the past two decades, however, this basin has experienced a series of pronounced environmental shifts, driven by a confluence of natural and anthropogenic factors (Keck et al., 2014; Troia et al., 2019). While studies have been done connecting functional traits to environmental drivers in the TNRB (Keck et al., 2014) and studies on temporal trends of functional traits over time (Comte, Carvajal-Quintero, et al., 2021), these ideas have not been combined for the TNRB. Dams, introduced species, toxic spills, mining, and agriculture have significantly affected the fish population. One significant consequence of these impacts is the fragmentation of the watershed, with approximately 40% of the riverine habitat in major tributaries being either impounded or modified by tailwater discharges (Neves & Angermeier, 1990). The isolation and stress experienced by these tributaries have led to the extinction of fish, mussels, and other aquatic fauna, with ongoing consequences expected to persist.

We aim to characterize the recent temporal trends of fish communities in the TnRB and the relative importance of anthropic stressors in driving these trends. To do this, we processed and analyzed a large and unique dataset of fish community samples collected by the Tennessee Valley Authority's (TVA) fish biomonitoring program from 1998 to 2021. Using open-access datasets and the published literature on biological and ecological traits of species (e.g., body size, reproductive characteristics, trophic position), We specifically investigate how the trait composition and identity of fish communities have changed over the last 20 years in the TnRB. By shedding light on these intricacies, we hope to provide valuable insights into the conservation and sustainable management of freshwater resources within the TNRB and beyond.

Methods

Time-series fish community data:

Fish data from the Tennessee Valley Authority's fish biomonitoring program, collected from 1998 to 2022, was used to acquire fish community samples. We used fish community data with repeated sampling over multiple years with more than ten years in range and at least four sampling events. Sites with multiple sets of coordinates due to rounding errors in the original data were standardized to the most precise measurement. We checked distances between coordinates under the same site to ensure no error in coordinate correction, with the maximum distance found being 0.0014. We retained sampling events occurring between March and August. There was one site that was sampled in both March and July, so we only retained the sampling events during the month of June, as the most common sample month was July. After filtering, 348 sites fit our criteria (Figure 1). On average, time series were sampled at 5.81 years (min: 4, max: 25, standard deviation (SD): 3.5) through a range of 18.98 years (min: 15, max: 25, SD: 2.92) and 30% completeness (min: 16.67%, max: 100%, SD: 14.89%) (Figure 2). Species names were validated and updated using FishBase through the *rfishbase* package (v4.0.0; Boettiger et al., 2012). Scientific names were cleaned by validating them with the current taxonomic names in Fishbase, and some had to be manually corrected. "Hybrid" individuals and species without specific epithet species were reduced taxonomically to their genus. Lampreys (Petromyzontiformes) and “unidentified” individuals were removed from the species list, leaving a total of 211 species after cleaning.

Species traits:

We selected six morphological and ecological traits (Table 1) hypothesized to respond to environmental change (Table 1). Trophic positions for each species were obtained from FishBase. The aspect ratio of the caudal fin (height of caudal fin^2/surface area of the caudal fin), log-transformed age at maturity (mean age in years of female at maturation), log-transformed fecundity (number of eggs), and egg size (mm) were obtained from Olden et al. 2021. The temperature affinity of each species was used for calculating the median temperature of occurrences available in the Global Information Facility (GBIF). Species names from all sources of species traits were validated with FishBase. We completed missing traits (3.72% missing values) using the average value of traits from congeneric species found in the TNRB. Out of the 7 traits for 211 species, 1,477 values remain missing; only 0.34% remain missing after averaging the values from congeneric species.

Estimating temporal trends in trait composition:

For each fish community surveyed (site x year), the community weighted mean (CWM) of each of the six traits was calculated. We averaged the trait values of the community using the relative abundance of the species as a weighting factor. Then, we estimated the temporal trends of each trait in each site across the TNRB using linear models by regressing CWM trait values against the year of sampling. We extracted the trend (year coefficient) and standard error as a measure of the strength of the rate of change (increase or decrease) of trait values and its uncertainty. Significance was determined based on a p-value of less than 0.05.

We implemented a meta-analytical approach using the *metafor* package to determine the overall trend and the heterogeneity of each trait in the basin as a whole (Viechtbauer, 2010). We used a random effects model with subbasins (Middle Tennessee-Elk, Middle Tennessee-Hiwassee, Upper Tennessee, French Broad-Holston, Lower Tennessee) as a random intercept to control for spatial non-independency in sites. All analyses were performed using R Statistical Software (v4.2.2; R Core Team, 2022). The tidyverse package in R was the primary package used to clean the data (v1.3.2; Wickham et al., 2019). All plots were made using the ggplot2 r package (v3.4.0; Wickham, 2016). Other R packages used in analysis were lubridate (v1.9.0; Grolemund & Wickham, 2011), sf (v1.0.9; Pebesma, 2018), stringr (v1.4.1; Wickham, 2022), viridis (v0.6.2; Garnier et al., 2021), and ggpubr (v0.5.0; Kassambara, 2022). Figure 3 overviews the methods of this study.

Environmental drivers of changes in trait composition:

We implemented a meta-regression to investigate the role of environmental changes in modulating the observed trends in trait composition. We focused on the effects of land cover and temperature changes at the local catchment of each site (COMID following the USGS National Hydrography Dataset). Temperature and land cover data were obtained from the streamcat dataset (Hill et al., 2016).

Results

Analysis of temporal trends in the different fish traits revealed substantial variability across the study period. For the TNrB overall, there were no significant trends for any traits. Significant changes in trait composition were observed across the study sites, reflecting spatial heterogeneity in the fish communities of the Tennessee River Basin (Figure 4). For all traits, the Test for Residual Heterogeneity was significant, indicating that there are more sources of variation that could impact the results of the model.

Aspect ratio showed a significant increasing trend in the Middle Tennessee-Elk and Upper Tennessee subbasins and a significant decreasing trend in the French Broad-Holston subbasin (Figure 5A). Trophic position showed a decreasing trend in the French Broad-Holston and Middle Tennessee-Hiwassee subbasins (Figure 5B). Age at maturity showed a significant decreasing trend in the French Broad-Holston, Upper Tennesee, and Lower Tennessee subbasins and a significant increasing trend in the Tennessee-Elk subbasin (Figure 5C). Fecundity showed a significant decreasing trend for the French Broad-Holston and Upper Tenessee subbasins (Figure 5D). Egg size had a significantly increasing trend in the French Broad-Holston, Middle Tennessee-Elk, and Upper Tennessee subbasins (Figure 5E). Temperature affinity showed a significant increasing trend for the Middle Tennessee-Hiwassee, Lower Tennessee, and Upper

Tennessee subbasins and a significant decreasing trend for the French Broad-Holston subbasin (Figure 5F).

Forest percent (Figure 6A) exhibited a significant positive effect on aspect ratio but a significant negative effect on trophic position, fecundity, and temperature affinity. In contrast, urban percent (Figure 6B) demonstrated a significant negative impact on aspect ratio and age at maturation while showing a significant positive impact on trophic position. The urban percent also had a significant positive effect on egg size and a significant negative effect on temperature affinity. Additionally, median temperature (Figure 6C) exerted a significant positive effect on aspect ratio and trophic position and a significant negative effect on age at maturation.

Discussion

The observed temporal trends in fish traits provide valuable insights into the dynamic nature of fish communities within the Tennessee River Basin and were all consistent with our hypotheses except for fecundity and egg size. The blending of the trends for each subbasin likely muddles the overall trend for the Tennessee River Basin, explaining why there are no significant trends overall.

The increasing trends in temperature affinity and aspect ratio in many subbasins, as well as the decreasing trend in trophic position, are consistent with our hypothesis and past literature. The decrease in trophic level is consistent, as vulnerability to the environmental conditions that accompany climate change increases with trophic level (Da Silva et al., 2023). The increasing trend in temperature affinity is consistent with our hypothesis and past literature suggesting the increasing dominance of warm-water (thermophilization) species in fish communities across different geographical and environmental spaces (Comte et. al., 2021). With alterations in land use and temperature, it is likely that species with a higher dispersal capacity, whose population dynamics may be influenced by environmental conditions at large-spatial scales, will be favored, which is consistent with our hypothesis and results (Radinger & Wolter, 2013).

The temporal trends of the life history traits are indicative of potential responses to changing environmental conditions. The consistent decrease in age at maturation underscores the importance of considering life history strategies in the context of environmental change and is consistent with past literature, as in unstable and challenging environments, fish species that reproduce sooner will likely be favored (Niu et al., 2023). The consistent increase in fecundity is associated with periodic species, which are typically migratory. These species may be sensitive to environmental changes because of their longer maturation time and their reliance on multiple habitats (Tamario et al., 2019). We hypothesized that egg size would decrease as species that put less energy into laying eggs and provide less parental care would be favored in an unstable environment. However, egg size was revealed to be largely increasing, which could be due to other factors not considered in the model.

The significant spatial variations in trait composition highlight the complexity of factors influencing fish communities across different sites. The temporal trends in fish characteristics are intricately linked to the environmental drivers of forest percent, urban percent, and median temperature at the study sites. As forest percent increases, a noteworthy negative trend in temperature is observed (Figure 7A), potentially attributed to the cooling effect of forests (Yin et al., 2022). Simultaneously, an increase in both median temperature and urban percent is associated with alterations in the aquatic habitat, leading to changes in species composition. This temperature increase appears to have a discernible impact on benthic species, contributing to a decline in their abundance (Cohen et al., 2016), which may be driving an increase in trophic position over time (Figure 7B). As urbanization intensifies, there is a notable negative trend related to trophic position, further hinting that this shift is likely affecting species occupying lower trophic levels, further contributing to the observed increase in trophic position (Figure 7C). Aspect ratio is positively correlated with median temperature (Figure 7D), which is consistent with past literature that fish with a higher aspect ratio will be favored due to the need for higher dispersal capacity that accompanies environmental conditions due to climate change (de Visser et al., 2023). These interconnected environmental drivers underscore the complexity of the relationships between habitat characteristics, temperature trends, and the ecological dynamics of fish communities over time.

There are some limitations to this study. First, the observed spatial heterogeneity in trait composition across subbasins indicates that local conditions play a significant role, yet the specific drivers of this variability are still to be thoroughly explored. Second, the two-decade temporal resolution may limit the capture of more extended ecological shifts, particularly those influenced by gradual changes. Additionally, other potential stressors, such as water pollution or habitat destruction, are not addressed in the meta-regression, which could also provide insights. The reduction of certain taxonomic categories and the basin-specific focus may limit the generalizability of the results to other freshwater ecosystems. Furthermore, this study aims to identify temporal trends but does not establish causation, highlighting the need for additional experimental studies to confirm the causal relationships between environmental stressors and specific trait modifications. Lastly, the potential influence of external factors, such as game fish dynamics and river size, on certain trait trends is acknowledged but warrants more in-depth exploration to enhance the study's overall robustness.

Thus, future research on the topic could include exploring other environmental factors, collecting more long-term data across a larger study area, and exploring other factors such as game fish. Overall, the findings of this study emphasize the need for integrated and adaptive management strategies to conserve the diverse fish communities of the Tennessee River Basin. Understanding the intricate relationships between temporal trends in fish traits and their underlying environmental drivers is crucial for the sustainable management and conservation of this ecologically significant freshwater ecosystem.

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Tables and Figures

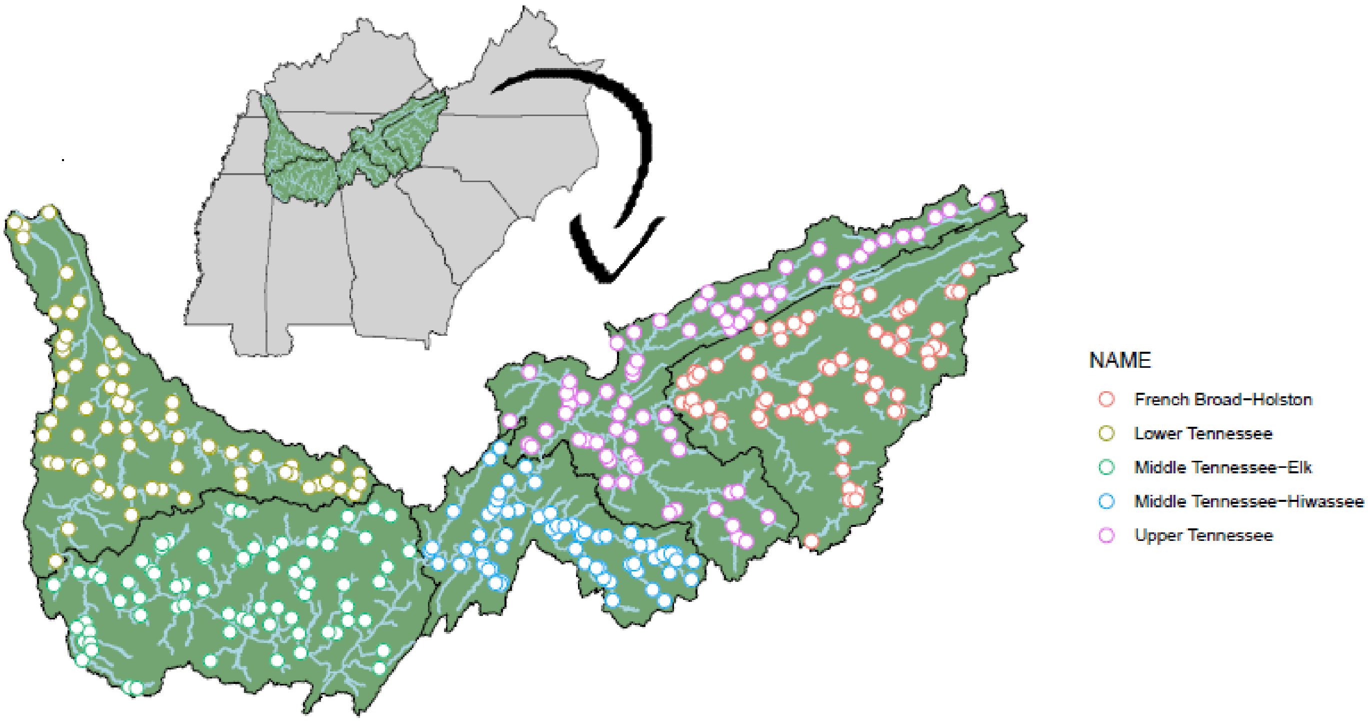


Figure 1. A map showing the sampling sites of the TVA monitoring program in the TNRB sites used for analysis inset with a map showing the TnRB (dark green) in reference to the southeast US.

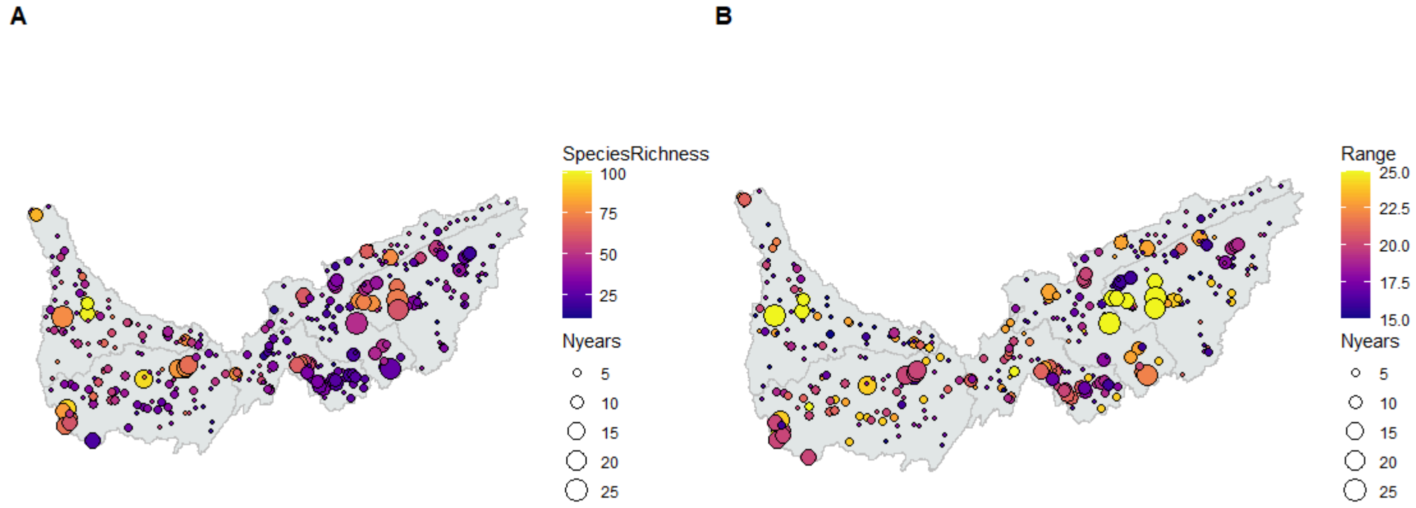


Figure 2. Sampling sites in the TnRB. A) Sites that are more complete are represented by yellow, and sites with a higher species richness are larger in size. B) Sites with a

longer range of years sampled are represented by yellow, and sites with higher number of years sampled are larger in size.

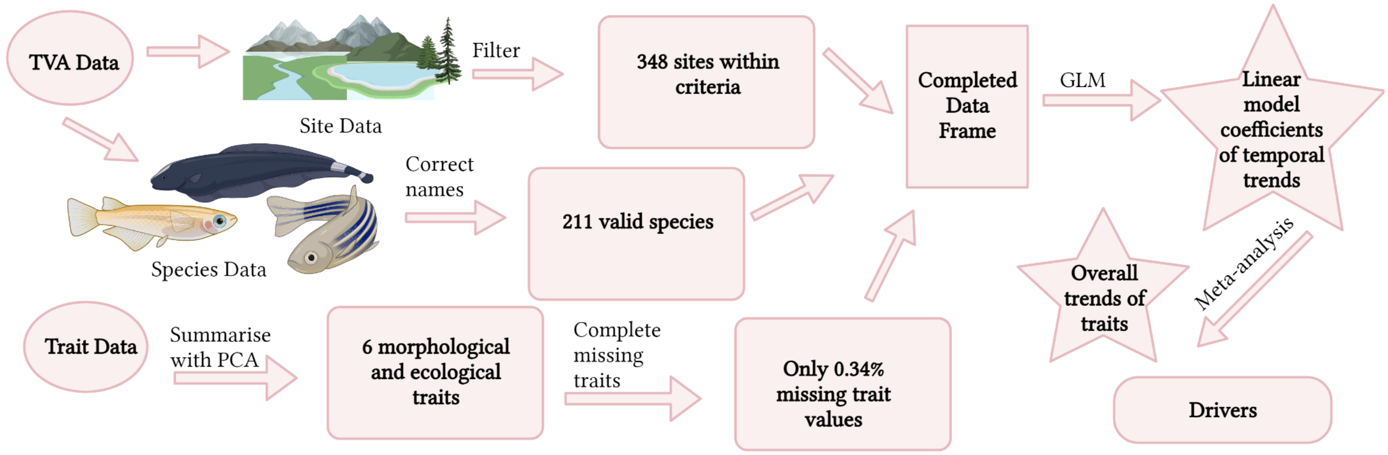


Figure 3. Workflow for estimating temporal trends in fish communities of the TnRB. Diagram created in BioRender.com.

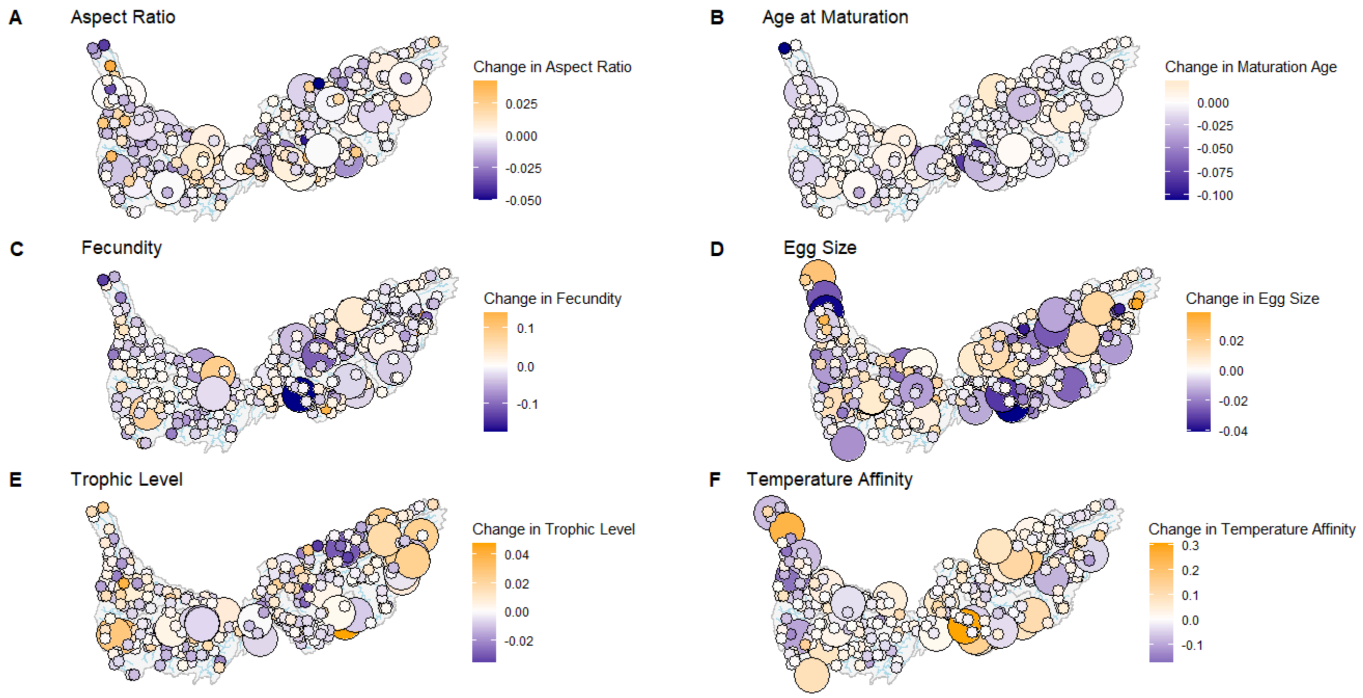
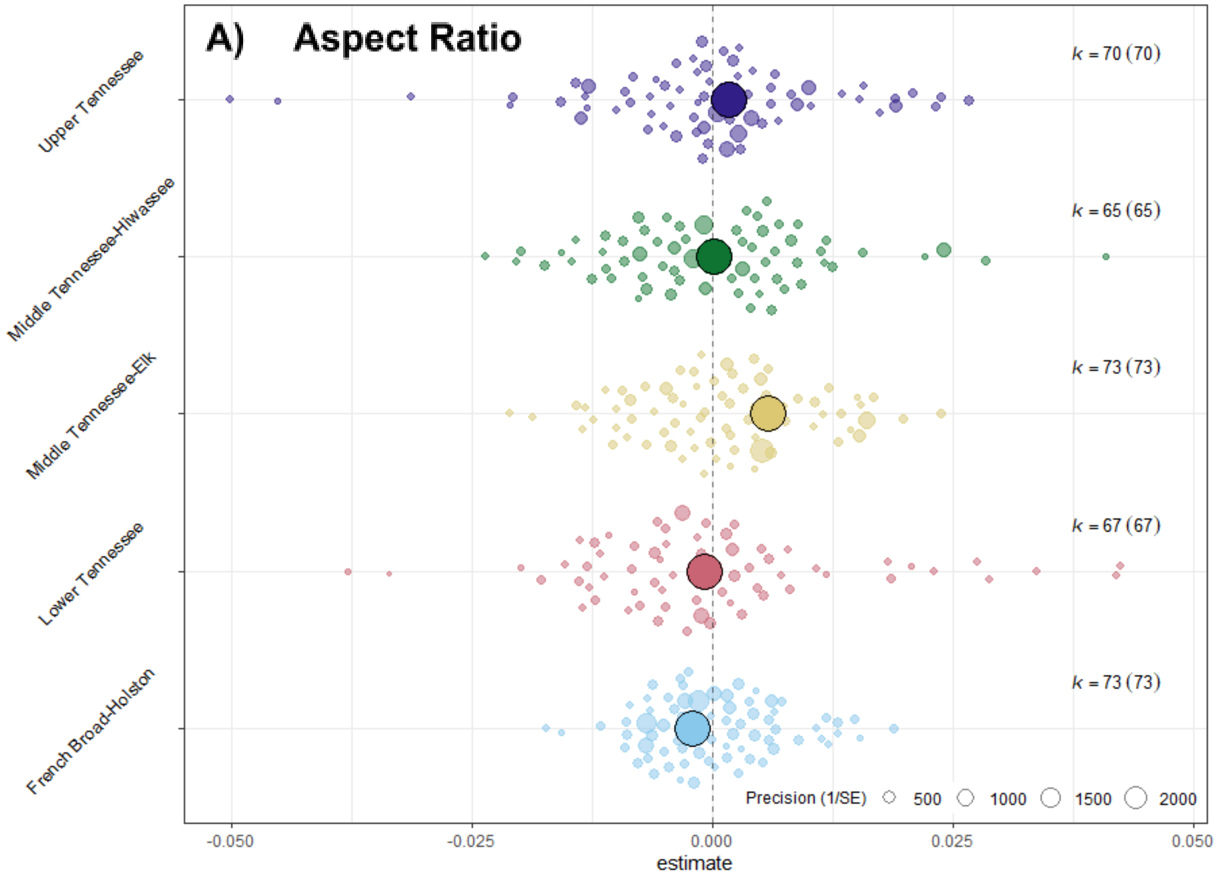
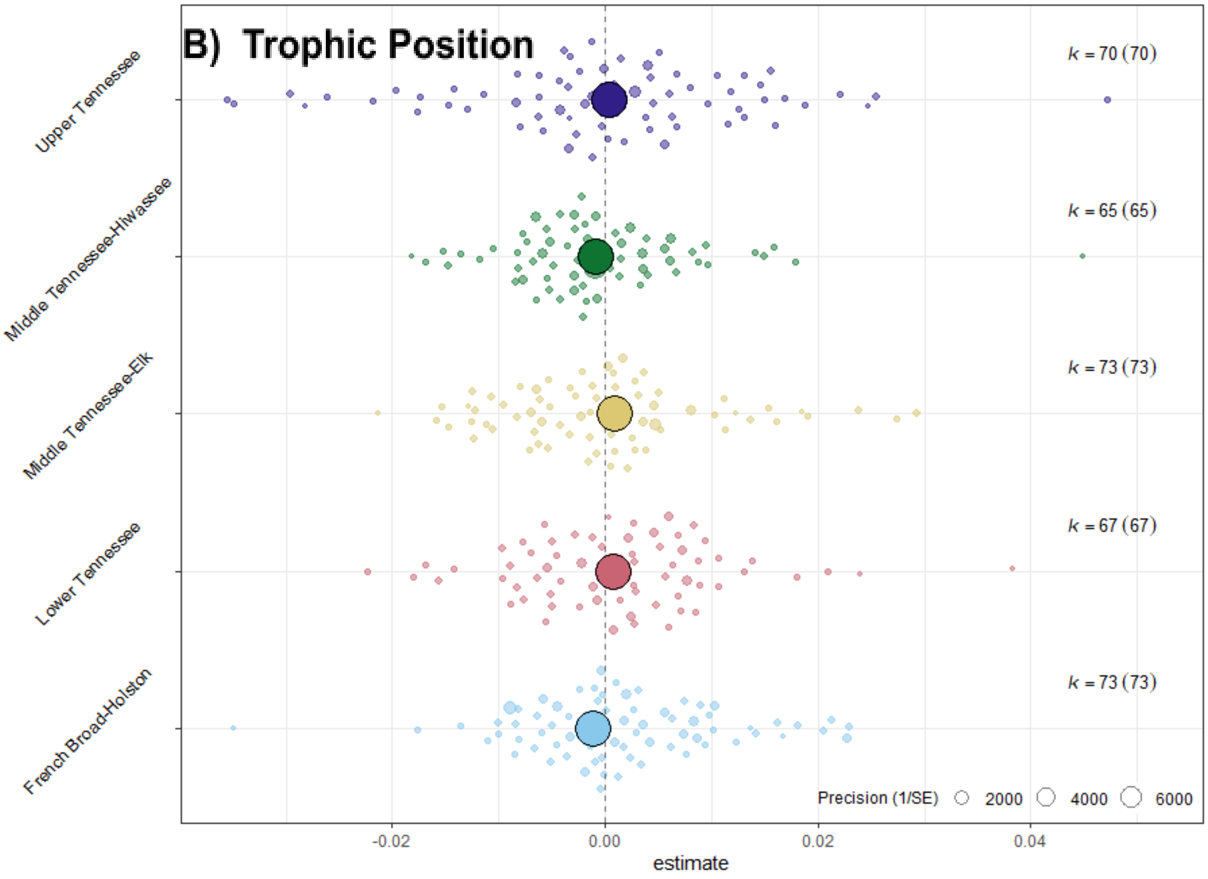
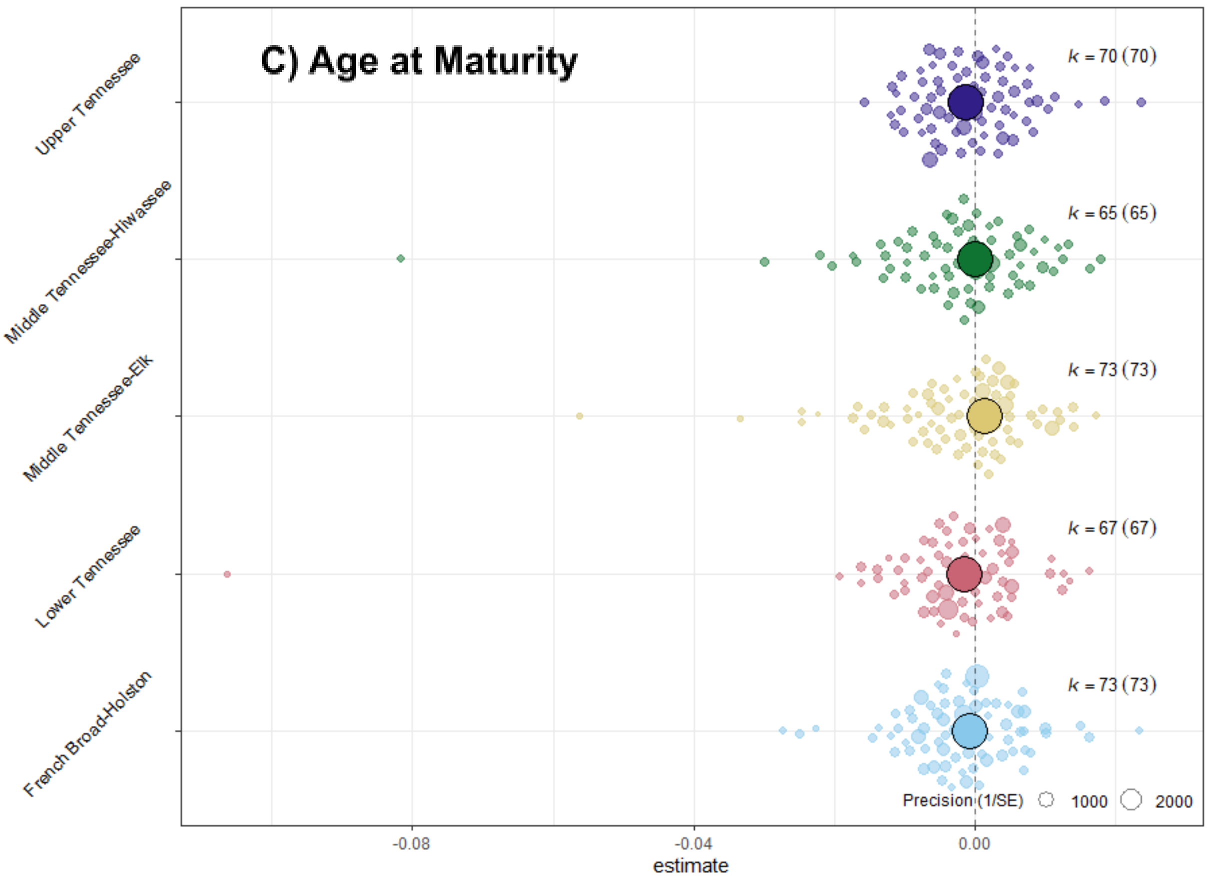
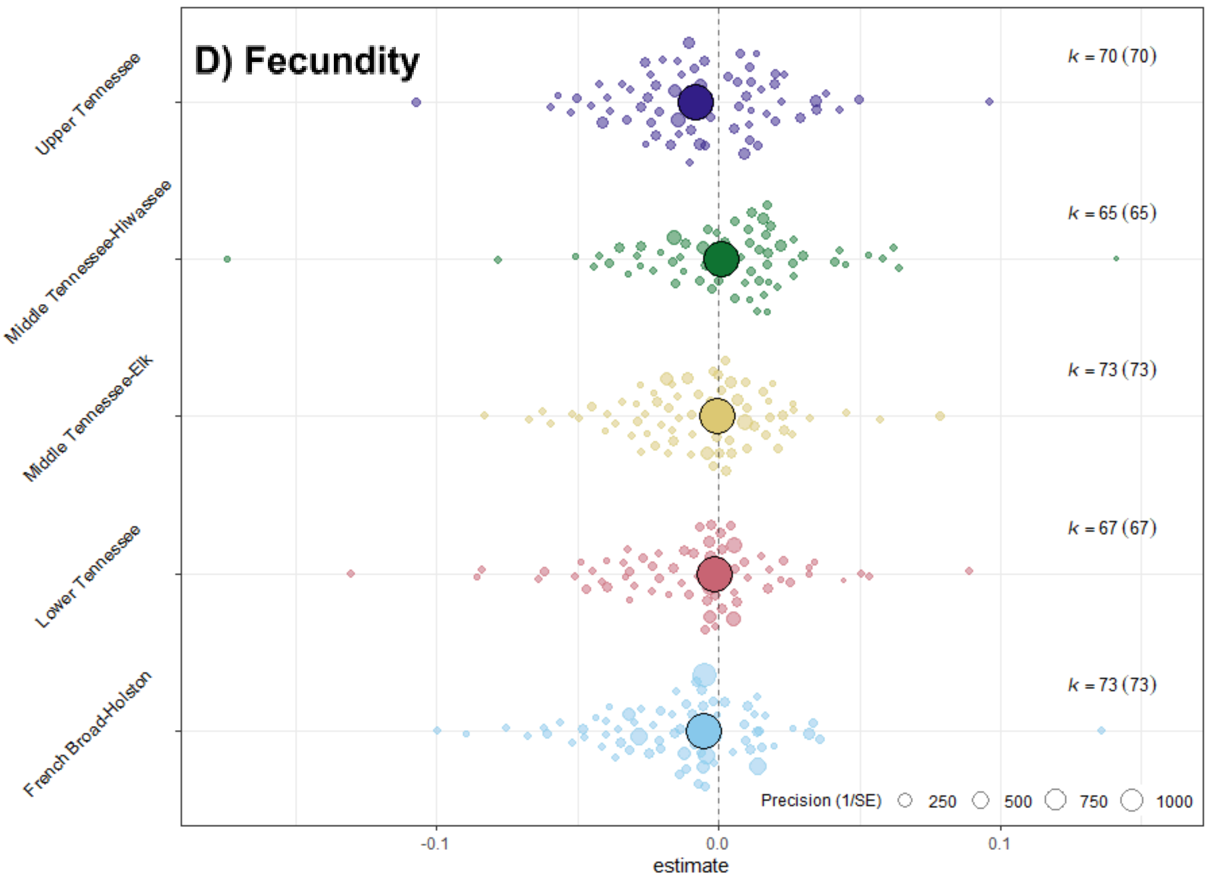


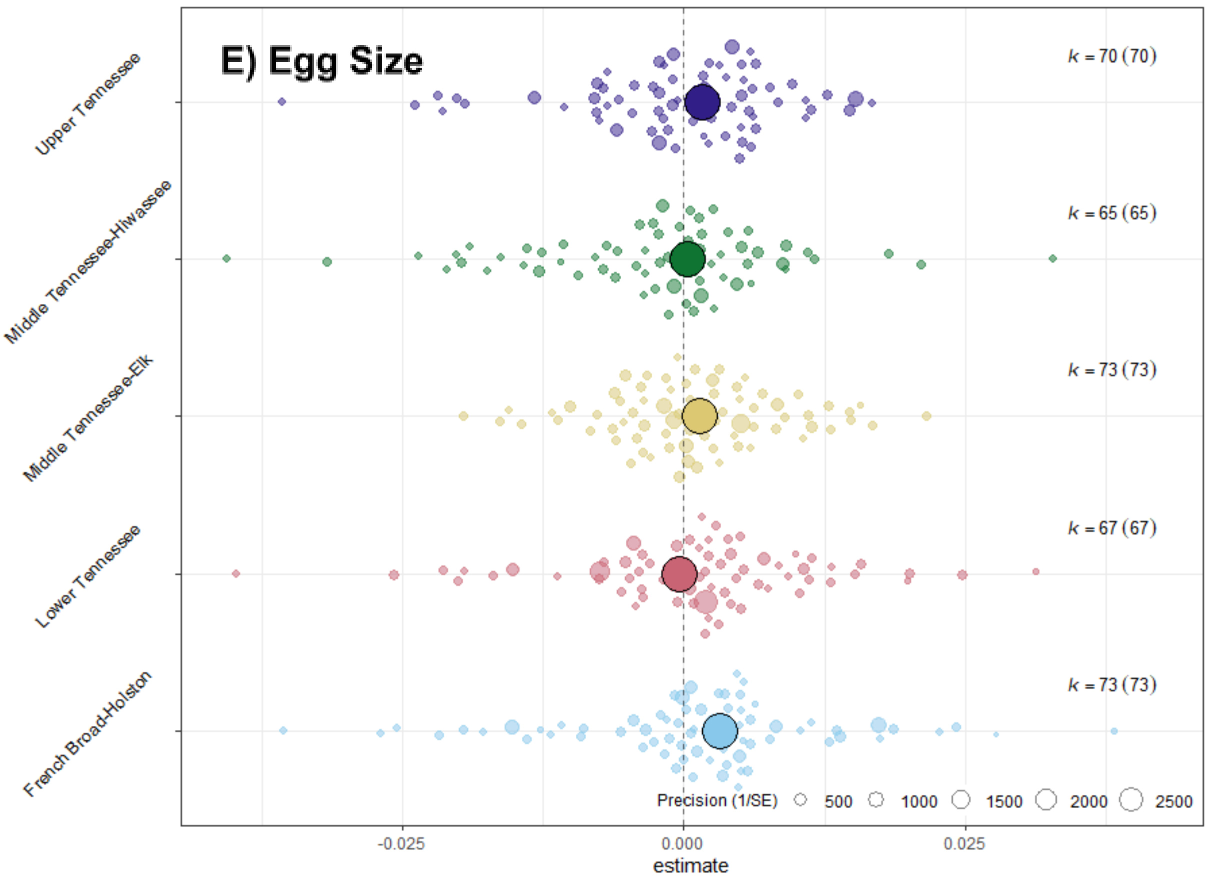
Figure 4. Temporal trends of each trait at each site in the TnRB. Large circles represent sites with a significant trend (p-value less than 0.05), while small circles represent sites that did not show a significant trend. Sites that are orange show a positive temporal trend, whereas sites that are purple show a negative temporal trend.




B) Trophic Position
Upper Tennessee
Middle Tennessee-Hiwassee
Middle Tennessee-Elk
Lower Tennessee
French Broad-Holston
k = 70 (70)
k = 65 (65)
k = 73 (73)
k = 67 (67)
k = 73 (73)
Precision (1/SE) 2000 4000 6000
-0.02
0.00
0.02
0.04
estimate


C) Age at Maturity
Upper Tennessee
Middle Tennessee-Hiwassee
Middle Tennessee-Elk
Lower Tennessee
French Broad-Holston
k = 70 (70)
k = 65 (65)
k = 73 (73)
k = 67 (67)
k = 73 (73)
Precision (1/SE)
1000
2000
-0.08
-0.04
0.00
estimate

D) Fecundity
Upper Tennessee
Middle Tennessee-Hiwassee
Middle Tennessee-Elk
Lower Tennessee
French Broad-Holston
k = 70 (70)
k = 65 (65)
k = 73 (73)
k = 67 (67)
k = 73 (73)
Precision (1/SE)
250
500
750
1000
-0.1
0.0
0.1
estimate


E) Egg Size
Upper Tennessee
Middle Tennessee-Hiwassee
Middle Tennessee-Elk
Lower Tennessee
French Broad-Holston
k = 70 (70)
k = 65 (65)
k = 73 (73)
k = 67 (67)
k = 73 (73)
Precision (1/SE)
500
1000
1500
2000
2500
-0.025
0.000
0.025
estimate

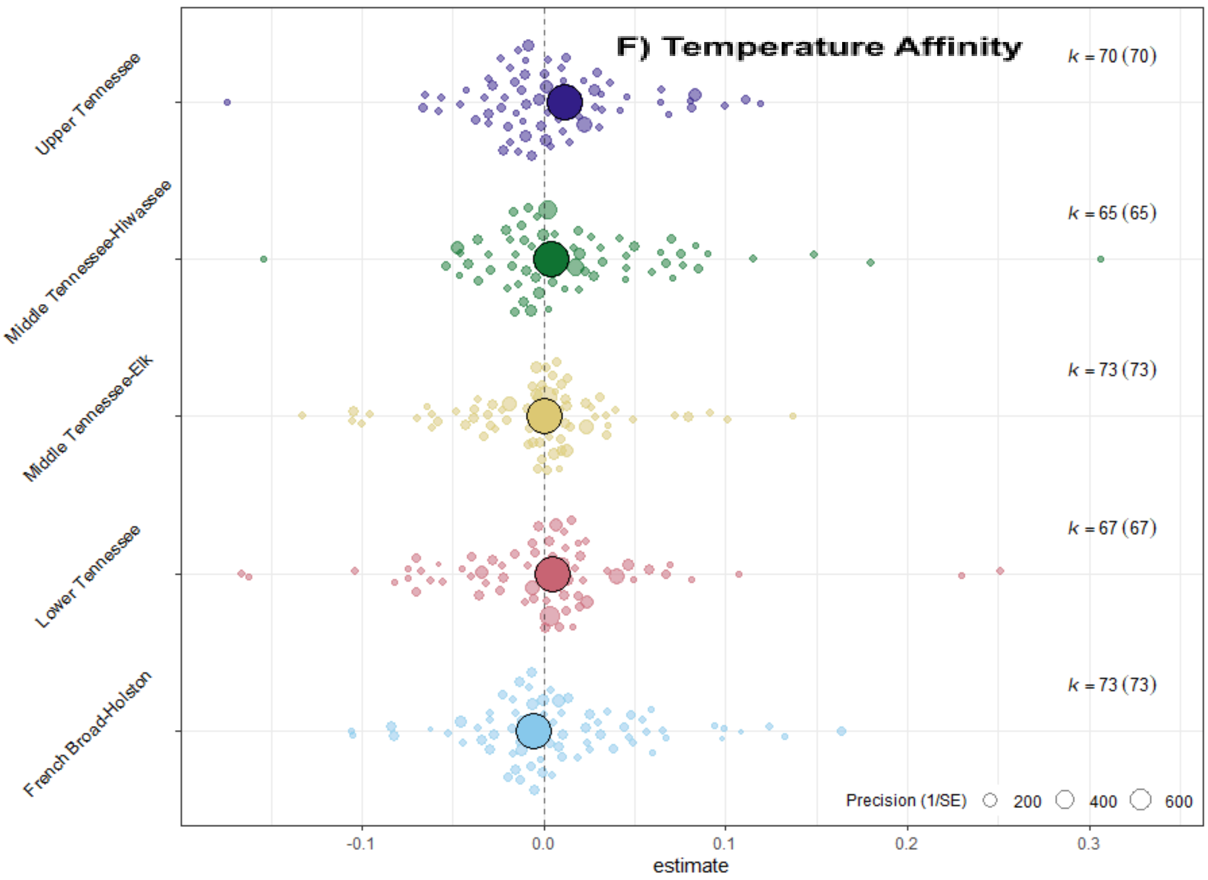
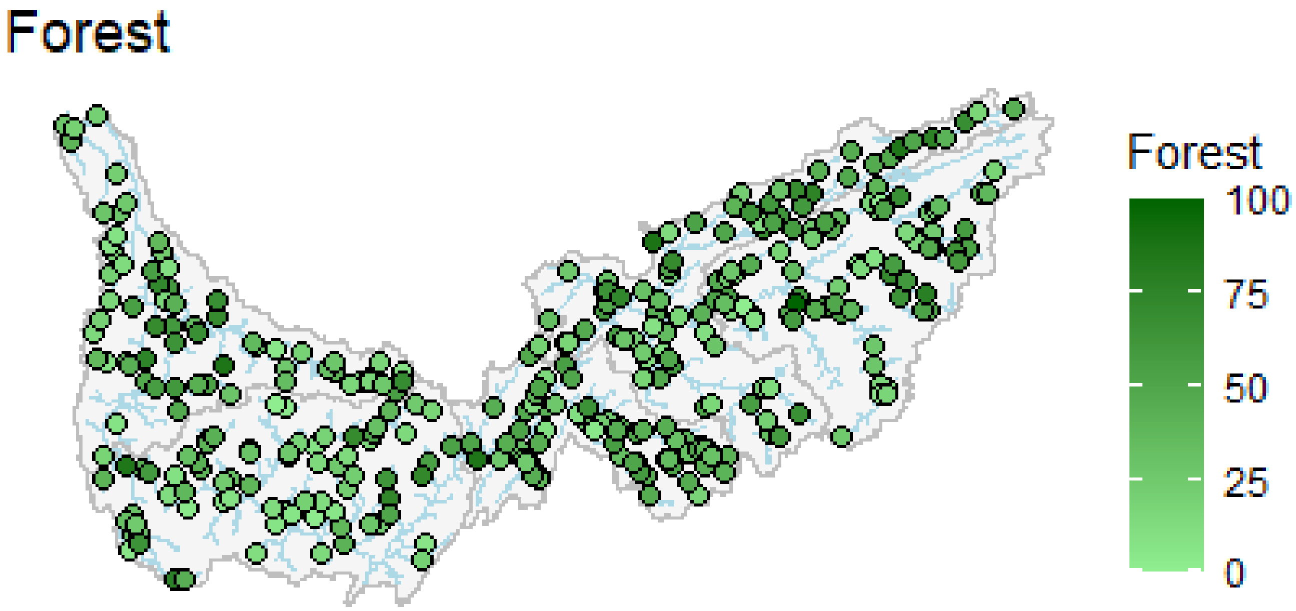


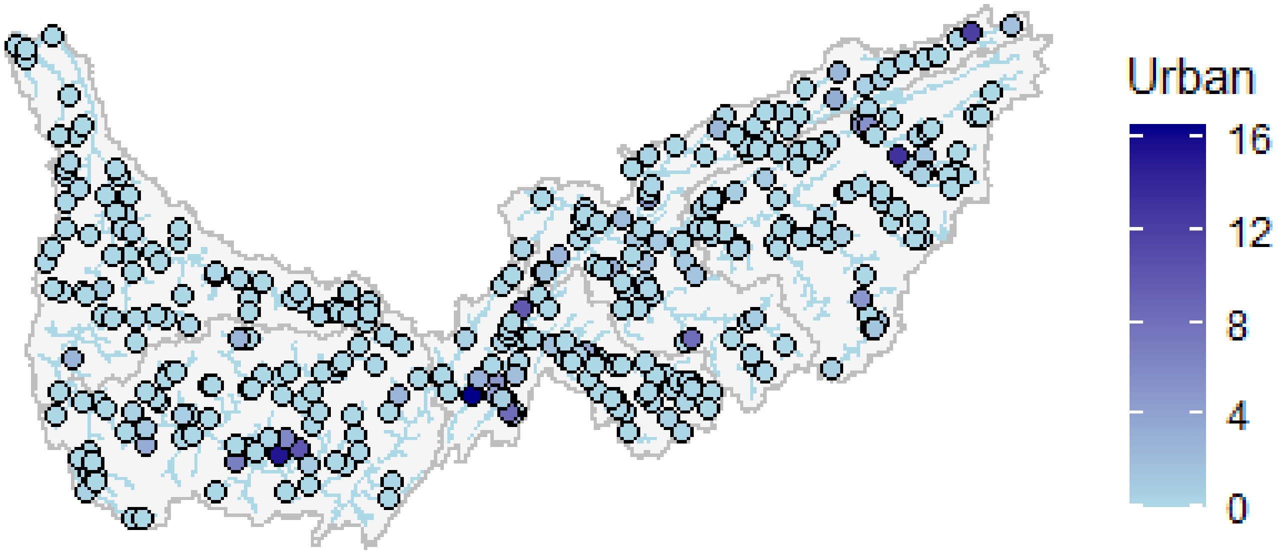
Figure 5. Plots of the estimate and confidence intervals for the trends of the 6 traits in the subbasins of the TnRB based on a random effects meta-analysis model. A) Aspect Ratio. B) Trophic Position. C) Age at Maturity. D) Fecundity. E) Egg Size. F) Temperature Affinity

A)



Forest

B)



Urban

C)

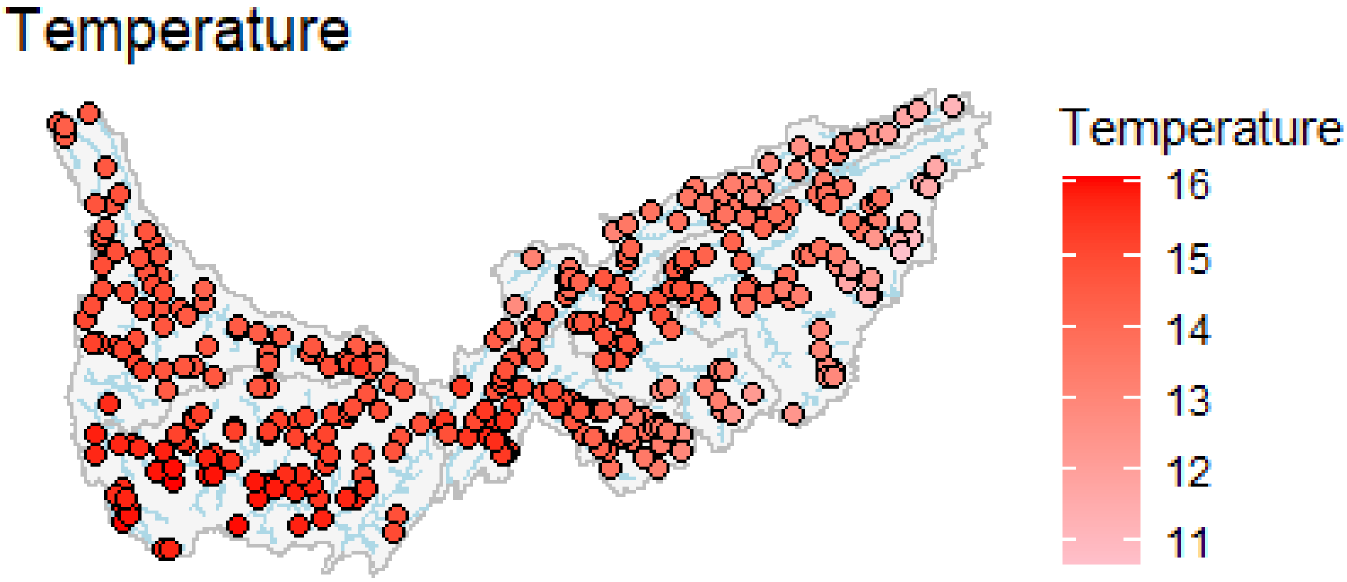
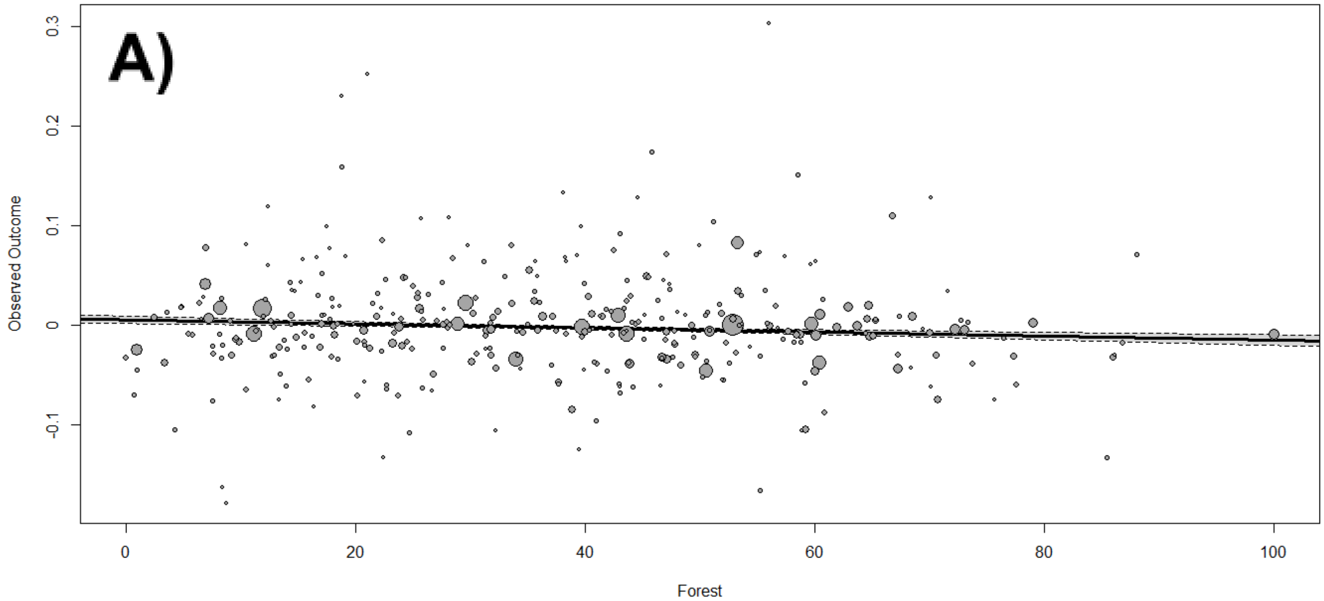
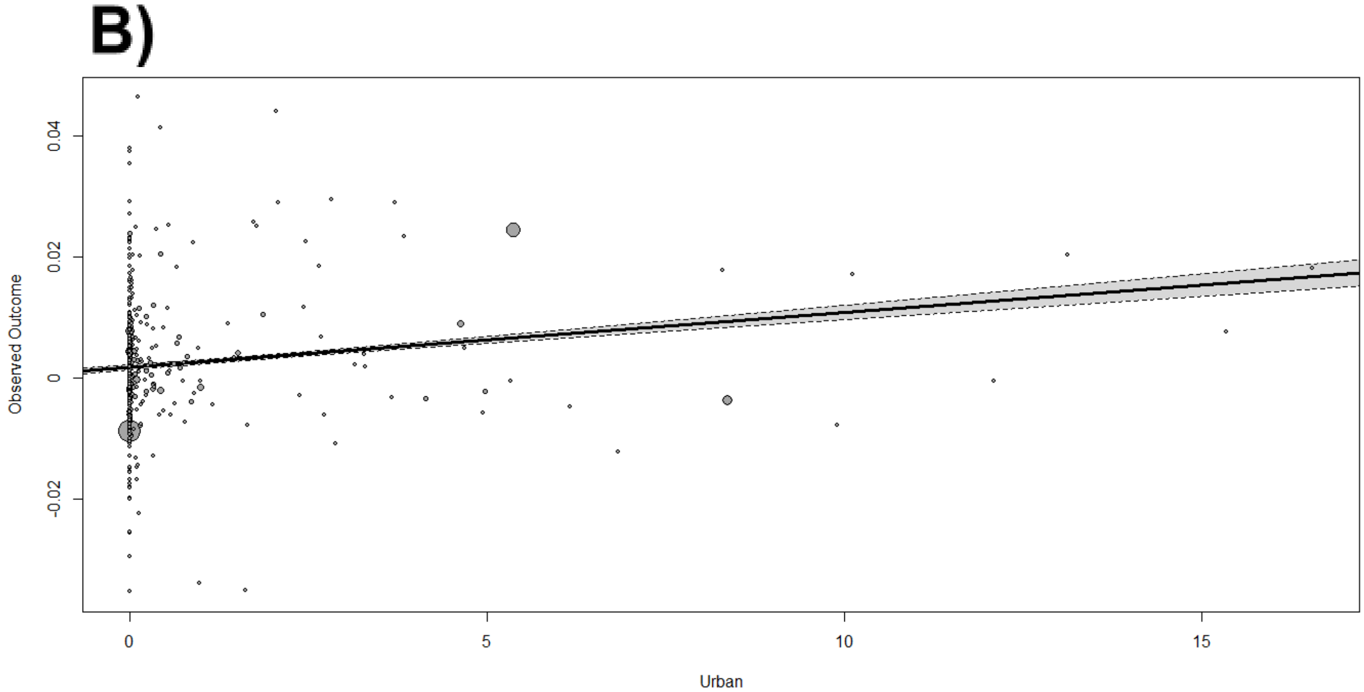


Figure 6: A map detailing the average values of environmental variables at each site. A) Forest percent. B) Urban %. C) Median Temperature.


A)
Observed Outcome
0.3
0.2
0.1
0
-0.1
0
20
40
60
80
100
Forest


B)
Observed Outcome
0.04
0.02
0
-0.02
0
5
10
15
Urban

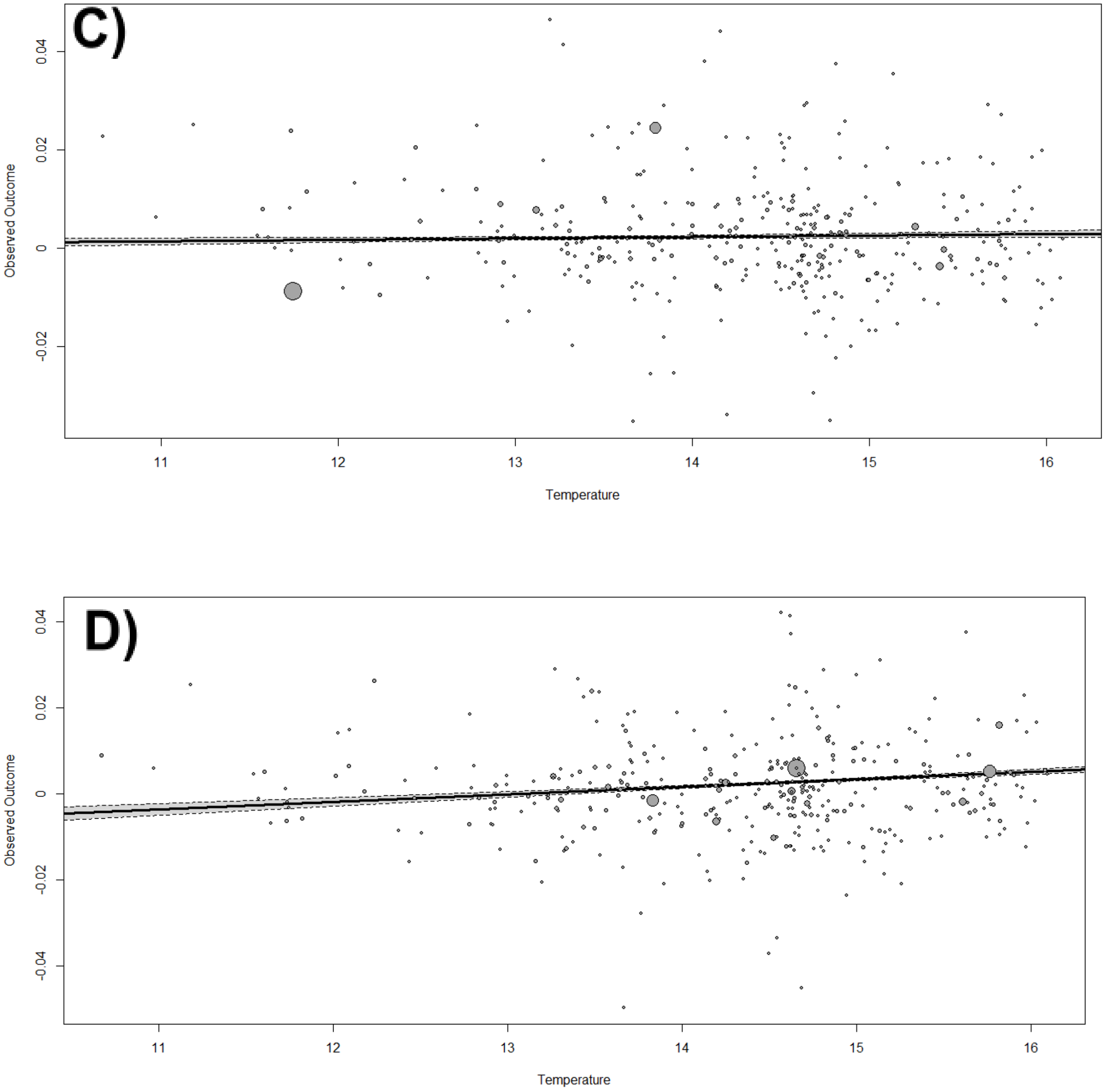


Figure 7: Plots detailing the relationship between the observed temporal trend (y) and the environmental driver (x). A) Median Temperature and forest percent. B) Trophic position and urban percent. C) Trophic position and median Temperature. D) Aspect Ratio and Median Temperature

Trait	**Environmental change driver**			**Expected mean temporal trend**
	Temperature	Forest cover (%) *	Urban cover (%)*	
Aspect ratio (Height/surface relationship of the caudal fin)	Increasing temperatures may display a decreasing trend in aspect ratio (Shapiro Goldberg et al.,2019)	A lower % forest should mediate an increase in aspect ratio due to the need for higher dispersal capacity	Same as left	Increasing trend
Age of maturity (Number of years)	Increasing temperature should mediate a decreasing trend in age at maturation (Nin et al., 2023)	Lower % forest should mediate a decreasing trend in age at maturation (Canosa et al., 2023)	Higher % urban should mediate a decreasing trend in age at maturation (Canosa et al., 2023	Decreasing trend: (want to have babies sooner if the environment is unstable): Opportunistic species with a low age of maturity are favored in more unstable and challenging environments.
Trophic position	Increasing temperature should mediate a decreasing trend in trophic level (Woodward et al., 2010)	Lower % forest should mediate an decreasing trend in trophic level (Wang et al., 2021)	Higher % urban should mediate a decreasing trend in trophic level (Wang et al., 2021)	Decreasing trend
Maxim fecundity (Number of eggs)	Increasing temperatures should mediate a decreasing trend in fecundity (Niu et al., 2023)	Lower % forest should mediate a decreasing trend in fecundity (Canosa et al., 2023	Higher % urban should mediate a decreasing trend in fecundity (Canosa et al., 2023	Increase (Species that have more offspring will be favored in an unstable environment)

				Decrease (A higher fecundity is associated with periodic migratory species, which may be more vulnerable to environmental change)
Egg size (mm)	Increasing temperatures should mediate a decreasing trend in egg size (Wooton et al., 2021)	Lower % forest should mediate a decreasing trend in egg size. (Winemiller et. al, 1992)	Higher % urban should mediate a decreasing trend in egg size. (Winemiller et. al, 1992)	Decrease (Species that put less energy into laying eggs/ less parental care will be favored in an unstable environment)
Temperature affinity (Comte et. al., 2021)	Increasing temperature should mediate an increasing trend in temperature affinity	Lower % forest should mediate an increasing trend in temperature affinity	Higher % urban should mediate an increasing trend in temperature affinity	Increasing trend

Table 1: Expected response of trait identity over time (Aspect ratio, Age of maturity, Trophic position, Maximum Fecundity, Egg size, Temperature affinity) in fish communities under environmental change in the Tennessee River Basin.