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Long-Term Shifts in Faunal Composition of Freshwater Mollusks in Spring-Fed Rivers of Florida

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Florida's freshwater spring and river ecosystems have been deteriorating due to direct and indirect human impacts. However, while the conservation and restoration strategies employed to mitigate these effects often rely on faunal surveys that go back several decades, the local ecosystem shifts tend to have much deeper roots that predate those faunal surveys by centuries or millennia. Conservation paleobiology, an approach which enhances our understanding of the past states of ecosystems, allows for comparison of modern faunal communities with those prior to significant human impacts. This study examines the historical record of freshwater mollusk assemblages from two spring-fed river systems, the Wakulla and Silver/Ocklawaha Rivers. Specifically, we compared fossil assemblages (latest Pleistocene - early Holocene) and live mollusk assemblages in the two targeted river systems. Bulk sampling of the fossil record (20 sites; 70 samples; 16,314 specimens) documented relatively diverse mollusk assemblages that consist of a suite of native freshwater species that is similar across the studied systems. In contrast, sampling of live communities (24 sites; 138 samples; 7,572 specimens) revealed depauperate species assemblies characterized by the absence of multiple native freshwater species commonly found in fossil samples, the widespread presence of introduced species, and dominance of brackish-tolerant species at the lower Wakulla River sites. Unlike fossil mollusk assemblages, live mollusk assemblages differ notably between the two river systems due to differences in relative abundance of introduced species (*Melanoides tuberculata* and *Corbicula fluminea*) and the presence of brackish-tolerant mollusks in the coastally influenced Wakulla River. The diverse, exclusively freshwater mollusk associations comparable across multiple river systems documented in the fossil record provide a historical perspective on the past state of freshwater river ecosystems complementing data provided by modern surveys. The conservation paleobiology approach used in this study reinforces the importance of considering the historical ecology of an ecosystem and the utility of the fossil record in providing a historical perspective on long-term faunal changes.

Keywords: mollusk, conservation paleobiology, fluvial, spring-fed, fossil, Quaternary, Florida

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INTRODUCTION

Humans have lived around and exploited Florida's springs and rivers for at least 13,000 years (Martin, 1966; Milanich, 1994). Modern development around freshwater springs began as early as the 1820s, initiating a long interval of gradually intensifying human impacts on water quality and ecosystem health (Revels, 1990; King, 2004). Today, these spring-fed river systems are increasingly threatened by invasive/introduced species (Bogan, 2006; Wingard et al., 2008; Nico et al., 2009; Kusnerik et al., 2020), excessive nutrient inputs (Turner and Rabalais, 1991; Turner et al., 2006; Liu et al., 2009; Heffernan et al., 2010; Bricker et al., 2014), vegetation loss/shifts (Brainwood et al., 2006; Lauretta et al., 2019), decreasing waterflow (Weber and Perry, 2006), sea level rise (Donoghue, 2011; Hong et al., 2014), and salinity fluctuations (Donoghue, 2011; Hong et al., 2014).

Recognizing these threats has prompted a renewed effort in recent years to study, conserve, and restore Florida's spring and river ecosystems through environmental surveys, restoration plans, and management actions by various state and private agencies (Howard T. Odum Florida Springs Institute, 2014; Wetland Solutions Inc, 2014; Florida Department of Environmental Assessment and Restoration, 2015). However, although anthropogenic impacts to spring ecosystems have been ongoing for centuries, live faunal surveys encompass only the last few decades (Odum, 1957; Knight, 1980, 1983; Munch et al., 2006). These recent efforts have documented conditions in already-altered ecosystems and, as such, provide critical data on changes that have taken place over the last several decades. However, we still lack critical information on the historical state of these ecosystems as they existed prior to substantial human impacts.

Conservation paleobiology is a rapidly emerging discipline that uses fossil or subfossil assemblages to provide historical ecological context for altered ecosystems. These approaches use fidelity or discordance between live, dead, and fossil assemblages, and other related methods, to recognize spatial and temporal biotic changes and provide long-term baseline assessments that can assist conservation and restoration efforts (e.g., Kowalewski et al., 2000; Jackson et al., 2001; Kidwell, 2007, 2013; Yanes, 2013; Hyman et al., 2019). Whereas these approaches have been used extensively in marine (e.g., Kidwell, 2007, 2013; Hyman et al., 2019), terrestrial (e.g., Yanes, 2013; Barnosky et al., 2017), estuarine/lagoonal (e.g., Barbieri et al., 2020), and freshwater (e.g., Alin and Cohen, 2004; Brown et al., 2005; Czaja et al., 2019) settings, spring-fed fluvial systems have been comparatively understudied. The primary goal of this study was to apply conservation paleobiological approaches to two spring-fed, fluvial systems in Florida. By comparing the compositional fidelity between live, dead, and fossil assemblages, the study aimed to document the faunal composition of freshwater molluscan communities prior to substantial human impacts, assess long-term ecological changes to those communities, and provide historical context for restoration/conservation efforts in local freshwater ecosystems.

Mollusks were used because their biomineralized shells have high potential for preservation in the freshwater fossil record, and their larger populations make collection of meaningful sample sizes feasible (Boardman et al., 1987; Kusnerik et al., 2020). Radiocarbon dates on individual fossil specimens (Kusnerik et al., 2020) revealed that freshwater mollusk shells from the studied rivers came predominantly from individuals that were late Pleistocene to early Holocene in age (18,217 to 7,087 cal BP), coinciding with hydrologic activation of flow in freshwater springs throughout Florida (Balsillie and Donoghue, 2011; Donoghue, 2011; O'Donoughue, 2015; Kusnerik et al., 2020). The radiocarbon dating efforts also indicate that mollusk assemblages were time-averaged over hundreds to thousands of years, constituting an averaged archive of long-term paleoecological conditions in the study system (Kusnerik et al., 2020). In more general terms, we focus here on mollusks because they are often used as environmental indicators (Williams et al., 2014), are sensitive to changes in water conditions (Montagna et al., 2008; Williams et al., 2014), can archive geochemical changes in aquatic habitats in their shell structure (Brown et al., 2005; Brainwood et al., 2006; Williams et al., 2014), and often provide ecosystem services including water filtration, substrate consolidation, and habitat structuring (Williams et al., 2014; Vaughn, 2018).

MATERIALS AND METHODS

Study Area and Field Methods

Samples were collected from two spring-fed river systems in Florida (**Figure 1**). These two systems, the Wakulla River and the Silver and Ocklawaha Rivers, were selected because they (1) vary in magnitude of human impacts, from severe (Silver River) to reduced (portions of the Wakulla River); (2) represent a range of salinity regimes, from fully freshwater (Silver/Ocklawaha Rivers) to coastally influenced (Wakulla River); and (3) afford easy logistical access.

The Wakulla River, located in Wakulla County, was sampled at 11 sites along the uppermost 11 km of the river (**Figure 1B**). Sites were distributed longitudinally starting at Wakulla Spring and continuing downstream to approximately 4 km upriver of the confluence of the Wakulla and St. Marks Rivers. Seven sites were located within Edward Ball Wakulla Springs State Park, which includes the headspring and uppermost 5 km of the river. The remaining four sites were in a publicly accessible portion of the lower river. In the sampled area, the Wakulla River is primarily meandering, with a short, braided section in the lower park. The river flows over undifferentiated Holocene and Pleistocene sediments, which overlie limestone deposits of the lower Miocene St. Marks Formation. Bottom substrates include peat, mud, silt, quartz sand, and limestone hardgrounds.

The Silver River, located in north-central Florida, Marion County, was sampled at eight sites along its 7.5 km length, from Mammoth Spring (main spring of the Silver Springs group) to the confluence with the Ocklawaha River (**Figure 1C**). An additional six sites were sampled on the Ocklawaha River, along a 3.5 km stretch downstream of the confluence point. The headspring and upper portion of the Silver River are located within Silver Springs State Park. Both the Silver and Ocklawaha are meandering rivers within the sampled regions. Both flow

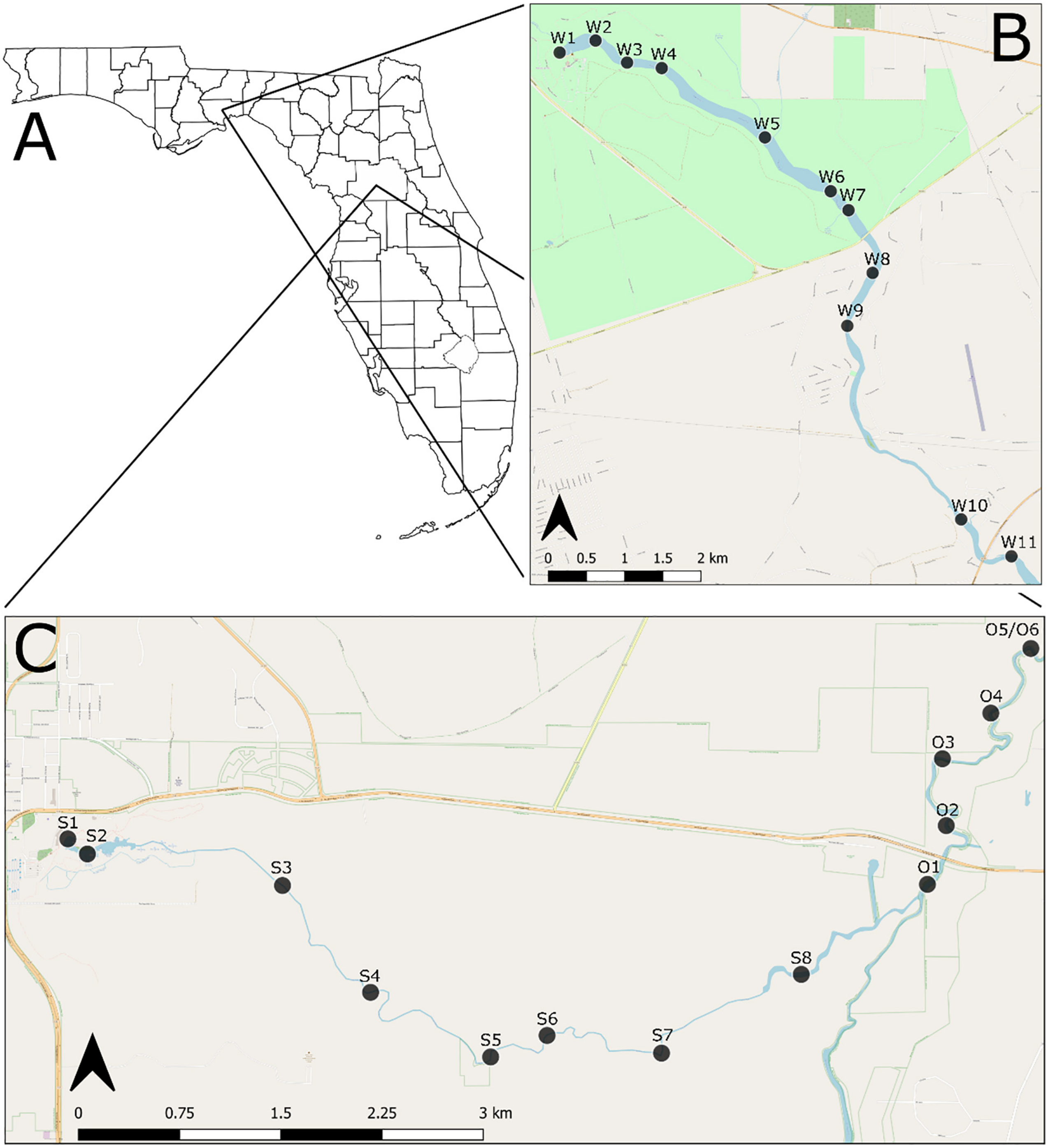

FIGURE 1 | **(A)** General location of the study area; **(B)** sampling sites along the Wakulla River; **(C)** sampling sites along the Silver and Ocklawaha Rivers. Sites along the Wakulla River begin with a "W," along the Silver River begin with an "S," and along the Ocklawaha River begin with an "O".

over undifferentiated Holocene and Pleistocene sediments, which overlie the upper Eocene Ocala Limestone. Bottom substrates include silts, clays, muds, limestone hardgrounds, and limestone cobbles.

Two types of samples were collected using SCUBA: live and fossil assemblages. Live assemblages represent timed (5, 10, or 15 min) hand-collection of living specimens by divers at all habitat types present at each site. Habitats typically included leaf litter, submerged logs, submerged vegetation, floating vegetation, mid-river channel sands and muds, and emergent shoreline vegetation. Live surveys were conducted between 2016 and 2019 (**Table 1**).

TABLE 1 | Latitude, longitude (datum WGS 84), and types of samples collected at each site.

Site name	River system	Latitude	Longitude	Sample types collected
S1	Silver	29.216081°	−82.052908°	Live
S2	Silver	29.215497°	−82.049989°	Fossil, Live
S3	Silver	29.212781°	−82.036519°	Live
S4	Silver	29.205769°	−82.029869°	Fossil, Live
S5	Silver	29.201492°	−82.020708°	Fossil
S6	Silver	29.203211°	−82.016700°	Fossil, Live
S7	Silver	29.202050°	−82.007550°	Fossil, Live
S8	Silver	29.209531°	−81.993578°	Live
O1	Ocklawaha	29.213119°	−81.987561°	Fossil, Live
O2	Ocklawaha	29.217000°	−81.986150°	Fossil, Live
O3	Ocklawaha	29.221622°	−81.986417°	Live
O4	Ocklawaha	29.224772°	−81.982617°	Fossil, Live
O5	Ocklawaha	29.228000°	−81.977919°	Fossil, Live
O6	Ocklawaha	29.227250°	−81.977581°	Fossil, Live
W1	Wakulla	30.235101°	−84.302516°	Fossil, Live
W2	Wakulla	30.236621°	−84.298099°	Fossil, Live
W3	Wakulla	30.23402°	−84.293837°	Fossil, Live
W4	Wakulla	30.233321°	−84.289278°	Fossil, Live
W5	Wakulla	30.225686°	−84.275377°	Live
W6	Wakulla	30.21805°	−84.264415°	Fossil, Live
W7	Wakulla	30.215557°	−84.263142°	Fossil, Live
W8	Wakulla	30.209782°	−84.260475°	Fossil, Live
W9	Wakulla	30.201076°	−84.26333°	Fossil, Live
W10	Wakulla	30.180287°	−84.248279°	Fossil, Live
W11	Wakulla	30.176231°	−84.24181°	Fossil, Live

Fossil samples were acquired through *in situ*, bulk collections of shell material from submerged vertical outcrops or small marl exposures on the riverbed. Outcrops and marls were composed of white to tan shell-rich clays with occasional layers of carbonate silt. Some outcrops contained a poorly indurated, dark-colored, organic-rich silt layer. When possible, outcrop exposures were sampled along a vertical profile, with each sample representing a rectangular cuboid spanning 5-10 cm vertically, 50-100 cm horizontally along the outcrop wall, and 10–20 cm perpendicularly into the outcrop exposure. Because of their size, smaller marl exposures on the riverbed were not sampled by cuboids, but rather, were sampled until one gallon of sediment was obtained. All samples were wet-sieved using 1 mm mesh sieves. Samples containing larger numbers of specimens were subsampled using strategies designed to minimize size-selection biases (sample splitters or multiple random subsets).

Death assemblages, the loose collection of shell material that accumulates in scours, divots, or similar erosional depressions on the river bottom, are also commonly used in conservation paleobiological research (e.g., Brown et al., 2005). While molluscan death assemblages were collected for this study, their complicated, multi-sourced provenance (Kusnerik et al., 2020) led to their exclusion from further analyses.

Specimen Description and Analysis

A total of 208 samples (live = 138, fossil = 70) were collected. Specimens were identified to the lowest taxonomic level, yielding 24,030 specimens that represent 20 taxa. Live samples from each site were pooled together into a single assemblage, regardless of their time of collection, to mitigate the effects of seasonal or annual variations in community composition. Bivalve counts were corrected to a minimum number of individuals by halving specimen counts. Two terrestrial gastropods (*Polygyra septemvolva* and *Daedalochila auriculata*) present in fossil assemblages were removed as live, terrestrial species were not sampled. The brackish-tolerant gastropod *Vitta usnea*, not observed in fossil samples, was removed as an ecological outlier in ordination analyses. Unionid mussels were also removed from ordination and pairwise comparisons because of taphonomic concerns, as their nacreous-aragonite shells do not preserve well in the fossil record (Simpson, 1899; Hinch and Green, 1988; Roper and Hickey, 1994; Wolverton et al., 2010; Williams et al., 2014). Exclusion of terrestrial species, freshwater mussels, and the brackish-tolerant *V. usnea* did not result in major changes to diversity analyses.

Samples with fewer than 20 specimens were removed from analyses to mitigate the effects of small sample sizes. Taxon abundance counts were standardized using double relativization (Wisconsin standardization). All analyses were performed in R (R Core Team, 2018) using custom written scripts and the package "vegan" (Oksanen et al., 2019). Sample-standardized richness was calculated using the "rarefy" function in the package "vegan" with the sample cutoff of 20 specimens. Ordination analyses were used to visualize compositional differences among samples and sample groups. Data were ordinated using Non-metric Multidimensional Scaling (nMDS) fit into $k = 2$ dimensions with 50 random restarts. Performance was assessed using stress values, with values < 0.2 deemed acceptable. Bray-Curtis similarity was used to quantify the compositional similarity between and within samples of both assemblage types and river systems. Differences in mean pairwise similarity between sample sets were statistically evaluated using randomization with distances resampled from pooled data to generate a sampling distribution under the null model of no difference in means. All p values were computed using the percentile approach with $p = I_E/I_T$, where I_E is the number of extreme iterations (i.e., number of replicate samples in which the resampled absolute difference in means exceeded the true absolute difference in means observed in the data) and I_T is a total number of iterations. When $I_E = 0$, p was reported as $p < 1/I_T$. Each randomization estimate was based on 10,000 iterations (pilot analyses indicated that estimates of p values stabilized at $I_T < 8{,}000$ iterations). Permutational multivariate analysis of variance (PERMANOVA), based on pairwise Bray-Curtis dissimilarities between samples, was conducted to assess whether sample groups were distinguishable statistically between assemblage types and river systems.

RESULTS

Fossil samples contained 16,314 specimens representing at least 14 species of freshwater mollusks (12 gastropods, one pea clam, and at least one species of unionid mussel) (**Table 2**). No introduced or brackish-tolerant species were present. Sample-standardized richness ($n = 20$ specimens) ranged from 2 to 6.38 (mean = 4.53). Whereas all fossil species were present in the samples from the Silver and Ocklawaha Rivers, only 11 were present in Wakulla River samples. The Wakulla samples were missing unionid mussels, indeterminate ancylid gastropods, and *Physella* sp., all of which were rare (n = 9, 3, and 2, respectively) in Silver/Ocklawaha fossil samples. Common species (> 10%) in both systems included *Planorbella duryi*, *Notogillia wetherbyi*, and *Elimia floridensis*. *Physella hendersoni* was also common in Silver/Ocklawaha samples. Pairwise similarities between fossil sites, estimated as Bray-Curtis similarity, ranged from 0.06 to 0.9 (mean = 0.51) for Wakulla fossil sites (**Figure 2A**) and from 0.04 to 0.88 (mean = 0.36) for Silver/Ocklawaha fossil sites (**Figure 2B**). Pairwise similarities between fossil sites compared across the two river systems ranged from 0 to 0.87 (mean = 0.3) (**Figure 2C**). The difference in mean pairwise similarity was statistically significant between within-Wakulla and within-Silver/Ocklawaha comparisons (**Supplementary Figure 1B1,B2** and **Table 3**). The difference was also statistically significant when comparing pairwise similarities within rivers to those between rivers (**Supplementary Figures 1F1,F2** and **Table 3**).

Pooling live samples by site produced a total of 25 samples, representing 7,572 specimens of 11 species (**Table 2**). These included eight native, freshwater mollusks (seven gastropods and one mussel), two non-native freshwater species (one gastropod and one clam), and one brackish-tolerant gastropod species (*V. usnea*). Sample-standardized species richness at sites ($n = 20$) ranged from 1 to 5.63 (mean = 2.63). Seven species were shared between the live communities of the Silver/Ocklawaha and Wakulla Rivers. An additional three species were present only in the Silver/Ocklawaha Rivers (*Callinina georgiana*, *Planorbella trivolvis*, and *Tarebia granifera*), whereas one species, the brackish-tolerant *V. usnea* was present only in the Wakulla River. Only one species was well represented (> 10%) in both systems, *E. floridensis* (Silver/Ocklawaha = 15.11% and Wakulla = 42.45%). In Silver/Ocklawaha River samples, other well represented species included unionid mussels (57.59%) and *Corbicula fluminea* (18.53%). In the Wakulla River, the common taxa were *Melanoides tuberculata* (29.56%) and *V. usnea* (23.19%). Between site Bray-Curtis similarity for live Wakulla samples ranged from 0 to 0.98 (mean = 0.36) and for the Silver/Ocklawaha samples ranged from 0.04 to 0.88 (mean = 0.36) (**Figures 2D,E**). Within-river mean similarity was not significantly different between the two systems (**Supplementary Figures 1A1,A2** and **Table 3**). Between-river similarity estimates ranged from 0 to 0.8 (mean = 0.17) (**Figure 2F**) and was significantly different from within-river similarity estimates (**Supplementary Figures 1E1,E2** and **Table 3**).

Live and fossil samples shared seven species (*E. floridensis*, *P. duryi*, *C. georgiana*, *N. wetherbyi*, *P. trivolvis*, *P. paludosa,* and unionid mussels) (**Table 2**). An additional seven freshwater species were present only in fossil samples (*P. hendersoni*, *Physella* sp., *Fluminicola dalli*, *Tryonia aequicostata*, *Lioplax pilsbryi*, *Pisidium* sp., and indeterminate ancylid gastropods). Four species were absent from the fossil record but present in live samples: the introduced *C. fluminea*, *T. granifera*, and *M. tuberculata* and the native, brackish-tolerant *V. usnea*. Compared to fossil samples, live samples were generally characterized by higher dominance, lower richness, and lower rarefied diversity (**Figure 3**). Similarity between fossil and live Wakulla samples ranged from 0 to 0.64 (mean = 0.11), and between fossil and live Silver/Ocklawaha samples from 0 to 0.62 (mean = 0.09) (**Figures 2G,H**). Mean similarity was statistically distinct between Wakulla live and Wakulla fossil samples, with fossil samples more similar and live samples less similar than expected (**Supplementary Figures 1C1,C2**). However, Silver/Ocklawaha live samples and Silver/Ocklawaha fossil samples were not statistically distinguishable in terms of pairwise similarities (**Supplementary Figures 1D1,D2**). Mean similarity between fossil samples from the two river systems was significantly more similar than expected, whereas live samples were significantly less similar (**Figures 4A,B** and **Table 3**).

To account for the impact of introduced species only in the modern (as they are absent from fossil assemblages), similar analyses were conducted with their exclusion. Although removing introduced species does not change pairwise comparisons of Bray-Curtis similarity for fossil samples, similarity among live samples within the same river system increases (**Supplementary Figures 5A,B**). Bray-Curtis similarity increases in the Silver/Ocklawaha Rivers (min = 0.27, max = 0.85, mean = 0.51). In the Wakulla, although the lower and upper river remains dissimilar from one another, overall mean similarity increases in live samples because of the high agreement

TABLE 2 | Abundances of aquatic species present in fossil and live samples compared to local and regional surveys.

		This study		**This study**		**Literature**				
		Fossil		**Live**		**Fossil**	**Live**			
Taxa	**Taxa categories**	**Wakulla**	**Silver/ Ocklawaha**	**Wakulla**	**Silver/ Ocklawaha**	**Florida**	**Wakulla**	**Wakulla-regional**	**Silver/ Ocklawaha**	**Silver/ Ocklawaha-regional**
Fluminicola dalli	Native, freshwater	+	++	–	–	present	NA	present	present	present
Ancylidae	Native, freshwater	–	+	–	–	NA	NA	NA	NA	NA
Elimia floridensis	Native, freshwater	+ ++	+++	+ ++	+++	present	present	present	present	present
Lioplax pilsbryi	Native, freshwater	+ +	+	–	–	NA	absent	present- select rivers	absent	absent
Notogillia wetherbyi	Native, freshwater	+ ++	+++	+ +	+	NA	NA	NA	NA	present
Physella hendersoni	Native, freshwater	+ +	++	–	–	present	present**	present	NA	present
Physella sp.	Native, freshwater	–	+	–	–	present	NA	NA	NA	NA
Pisidium sp.	Native, freshwater	+	+	–	–	present	NA	NA	NA	NA
Planorbella duryi	Native, freshwater	+ ++	+++	+	–	present	NA	present	NA	present
Planorbella trivolvis	Native, freshwater	+	++	–	+	present	NA	present	NA	present
Pomacea paludosa	Native, freshwater	+ +	++	+	+ +	present	present***	present	present	present
Tryonia aequicostata	Native, freshwater	+	++	–	–	present	absent	absent	absent	present
Unionidae	Native, freshwater	–	+	+	+ + +	present	present	present	present	present
Callinina georgiana	Native, freshwater	+ +	++	–	+ +	present	NA	present	NA	present
Corbicula fluminea	Introduced, freshwater	–	–	+ +	+++	absent	present	present	present	present
Tarebia granifera	Introduced, brackish-tolerant	–	–	–	+	absent	NA	absent	NA	present
Melanoides tuberculata	Introduced, brackish-tolerant	–	–	+ ++	+	absent	NA	present	NA	present
Vitta usnea	Native, brackish-tolerant	–	–	+ ++	–	present*	NA	present	NA	NA

*Abundances of species in this study are represented as (1) - absent, (2) + < 1%, (3) + + 1-10%, or (4) + + + > 10%. Local and regional literature reviews document the taxa as present, absent, or NA (data not available) with additional information presented where appropriate. *Present as Neretina usnea, **Documented as present in a 1956 survey, ***Extirpated from the Wakulla River in the 1990s and anthropogenically reintroduced in the 2000s and 2010s.*

in the upper river (min = 0.03, max = 1, mean = 0.71). Removing introduced species does not dramatically change similarity between rivers (min = 0.03, max = 0.8, mean = 0.27) (**Supplementary Figure 5C**).

In ordination space, fossil samples plot as a cloud with some separation along nMDS1 and tight clustering along nMDS2 (**Figure 5**). Whereas there is some clustering by river system within the cloud, fossil samples from the different rivers broadly overlap. Live Wakulla River samples plot at high nMDS1 and high nMDS2 scores, distinct from nearly all fossil and live Silver/Ocklawaha River samples (**Figure 5**). Live Silver/Ocklawaha River samples mostly plot at high nMDS1 and low nMDS2 scores, distinct from all fossil and live Wakulla River samples. Whereas the majority of species plot within the cluster of fossil samples, three species do not. Two species, the introduced *M. tuberculata* and native *E. floridensis*, plot at higher nMDS1 and nMDS2 scores, similar to the Wakulla live samples, in which both taxa are abundant. The introduced *C. fluminea* scores are similar

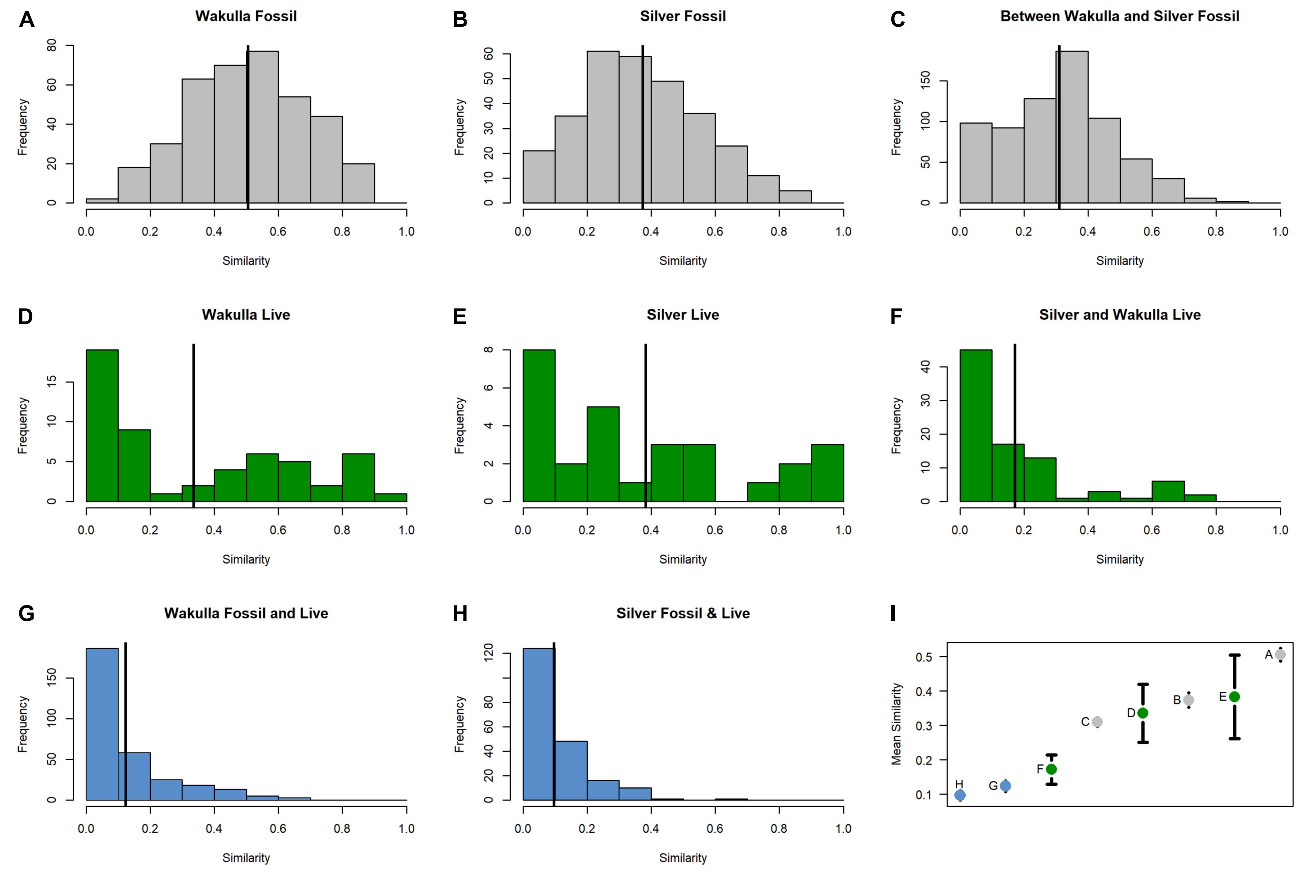

FIGURE 2 | Pairwise comparisons of Bray-Curtis similarities between fossil (gray) samples **(A)** within the Wakulla River, **(B)** within the Silver and Ocklawaha Rivers, **(C)** between the Wakulla, Silver, and Ocklawaha Rivers, between live (green) samples **(D)** within the Wakulla River, **(E)** within the Silver and Ocklawaha Rivers, **(F)** between the Wakulla, Silver, and Ocklawaha Rivers, and between fossil and live (blue) samples **(G)** within the Wakulla River and **(H)** within the Silver River. **(I)** Mean similarities of the eight pairwise comparisons with 95% confidence intervals. **(A–H)** represent their respective panels in **Figure 2**.

TABLE 3 | Probability of observed mean pairwise similarity between sample sets evaluated using randomly generated null model of no difference in means.

Comparison	*p*-value
Wakulla and Silver/Ocklawaha within river live to live similarity	0.736
Wakulla and Silver/Ocklawaha within river fossil to fossil similarity	< 0.0001*
Wakulla River live to fossil similarity	< 0.0001*
Silver/Ocklawaha River live to fossil similarity	0.6554
Wakulla and Silver/Ocklawaha within river live to Wakulla and Silver/Ocklawaha between river live	< 0.0001*
Wakulla and Silver/Ocklawaha within river fossil to Wakulla and Silver/Ocklawaha between river fossil	< 0.0001*
Wakulla and Silver/Ocklawaha between river fossil to Wakulla and Silver/Ocklawaha between river live	< 0.0001*

*$p < 0.05$.

to most live Silver/Ocklawaha samples, at high nMDS1 and low nMDS2 scores. PERMANOVA indicates that the two assemblage types and two river systems are significantly different ($F = 7.3$, $p < 0.001$).

When ordination is restricted to only fossil assemblages, samples plot as a broadly overlapping cloud (**Figure 6**). Wakulla and Silver River samples show substantial overlap with one another, with a weak separation along nMDS2. Most Ocklawaha River samples plot within a distinct cluster, separating from the broader Silver and Wakulla River cluster along nMDS1. A number of Ocklawaha River samples, however, still overlap with those of the other rivers. Species scores for *L. pilsbryi*, *Pomacea paludosa*, and *C. georgiana* are generally similar and overlap with the largest cluster of fossil Wakulla River samples. Two species, *E. floridensis* and *N. wetherbyi*, plot in a region of ordination space where Wakulla and Silver River samples overlap. *Planorbella duryi*, *P. trivolvis,* and *P. hendersoni* plot at similar scores as the cluster of Ocklawaha River samples.

If introduced species are removed from analyses and ordinations, live samples still exhibit higher dominance, lower

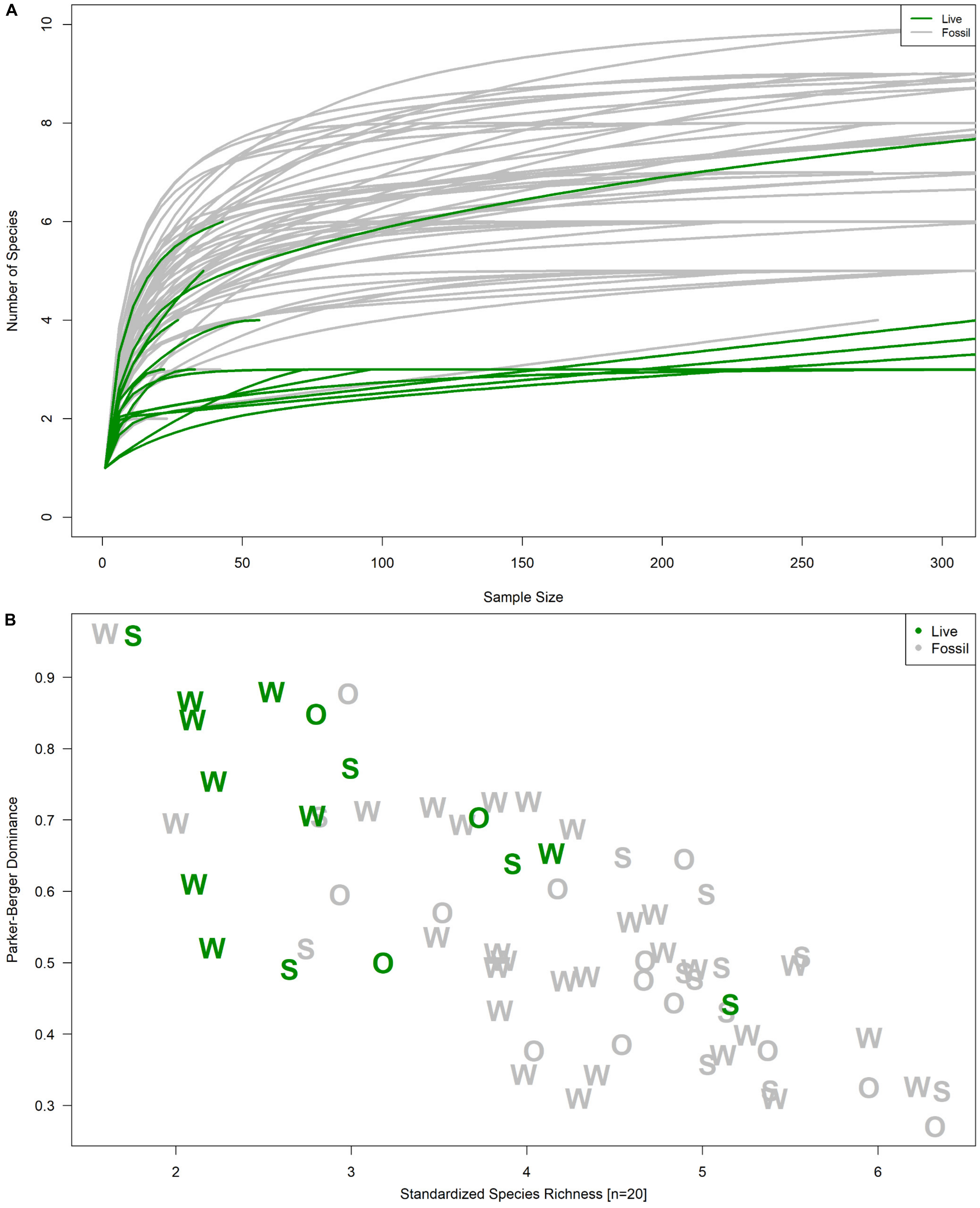

FIGURE 3 | (A) Rarefaction curves and **(B)** richness-dominance plot and of fossil (gray) and live (green) samples. Letters in **(B)** correspond to a sample's river system: "W" for Wakulla, "S" for Silver, and "O" for Ocklawaha.

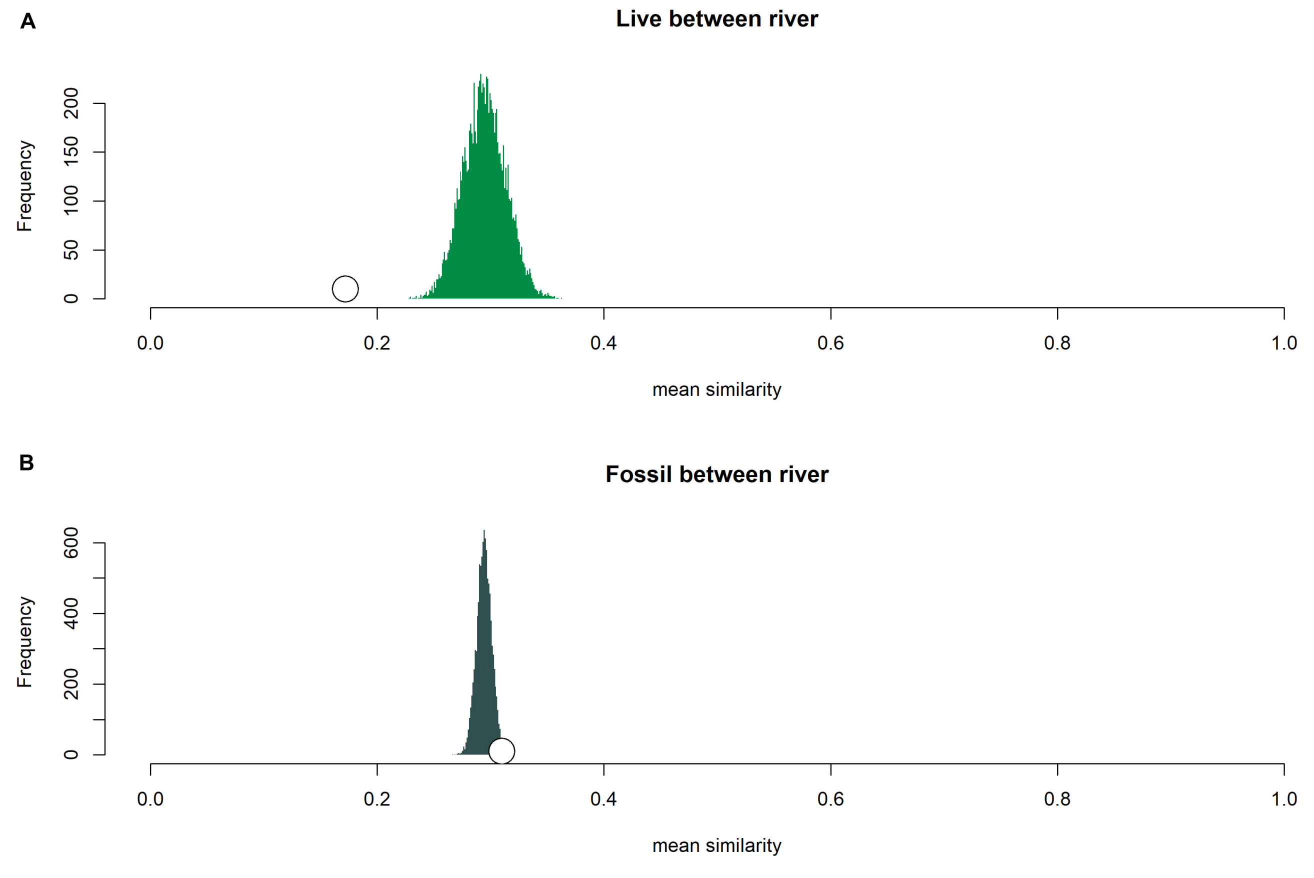

FIGURE 4 | Comparison of expected mean similarity distributions (based on randomization under the null model that all pairwise comparisons came from the same underlying statistical population) with observed mean similarity values for within river **(A)** live samples and **(B)** fossil samples. Open white circle is the observed mean similarity for the given set of comparisons.

richness, and lower rarefied diversity than fossil samples (**Supplementary Figures 2, 3**). In ordination space, there is still separation between the live samples of both river systems primarily along nMDS2 (**Supplementary Figure 4**). Whereas like Wakulla samples still separate from fossil samples along nMDS1, many live Silver/Ocklawaha samples instead now separate along a combination of nMDS1 and nMDS2. Among species scores, *E. floridensis* plots distinctly separate, roughly coinciding with the clustering of live Wakulla samples, likely due to their heavy abundance in these samples. Three species, *C. georgianus, P. paludosa,* and *L. pilsbryi* separate from other species scores, plotting similarly to one another in the same ordination space as a heavy cluster of fossil Wakulla samples and relatively near live Silver and Ocklawaha samples.

Comparative Local and Regional Faunal Context

Regional, county-level, or watershed-level occurrences are often recorded for live mollusks. However, except for species of special ecological interest (i.e., endangered species, harmful invasives, critical food source for endangered birds, etc.), live mollusks are rarely documented *via* quantitative sampling and are often relegated to passing mentions in larger faunal surveys. Because their shells have high preservation potential, however, mollusks are more readily recorded in the freshwater fossil record of Florida, and often documented in detail when found in fossil deposits (Portell et al., 1995; Karrow et al., 1996; Auffenberg et al., 2006; Kittle and Portell, 2010; Portell and Kittle, 2010). Below, we compare general abundances of species in our study with their previously published records in present-day local and regional river systems as well as in fluvial (or fluvial-adjacent) Pleistocene fossil deposits of Florida.

The comparative data from other fossil sites in the region includes three sites that are summarized here briefly. The first fossil locality, the Page-Ladson site, lies on the Aucilla River in Jefferson County, approximately 30 km SE of the sampled Wakulla River sites (Auffenberg et al., 2006). Fossiliferous deposits containing freshwater mollusks were radiocarbon dated to between ∼12,500 and 9,950 BP (Auffenberg et al., 2006; Webb and Dunbar, 2006). The paleoenvironment was interpreted as having been shallow (< 3 m) and freshwater (Auffenberg et al., 2006). The second locality, the Oldsmar site in Pinellas County, contains a non-marine, fossiliferous clay and sand layer of the late Pleistocene Fort Thompson Formation (Karrow et al., 1996) and lies approximately 150 km SW of sites sampled along the Silver

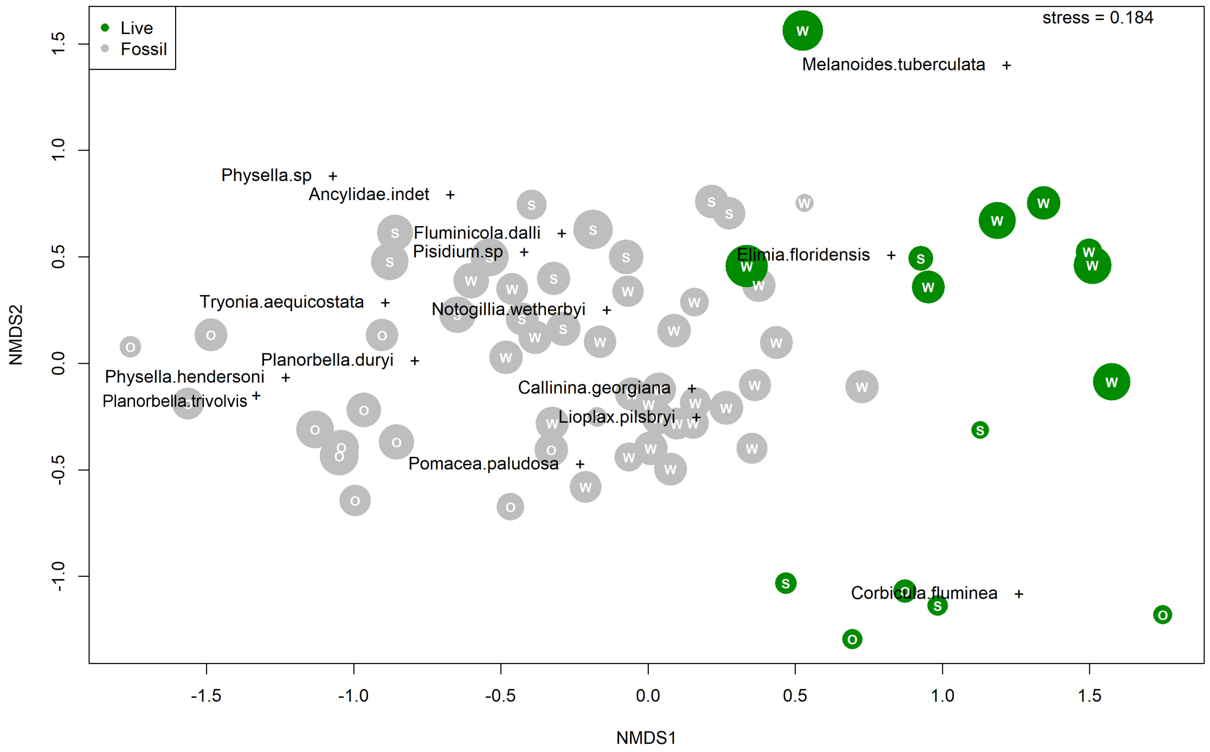

FIGURE 5 | Non-metric Multidimensional Scaling (nMDS) species and sample scores. Fossil samples in gray and live samples in green. Letters correspond to a sample's river system: "W" for Wakulla, "S" for Silver, and "O" for Ocklawaha. Points scaled by number of specimens in each sample.

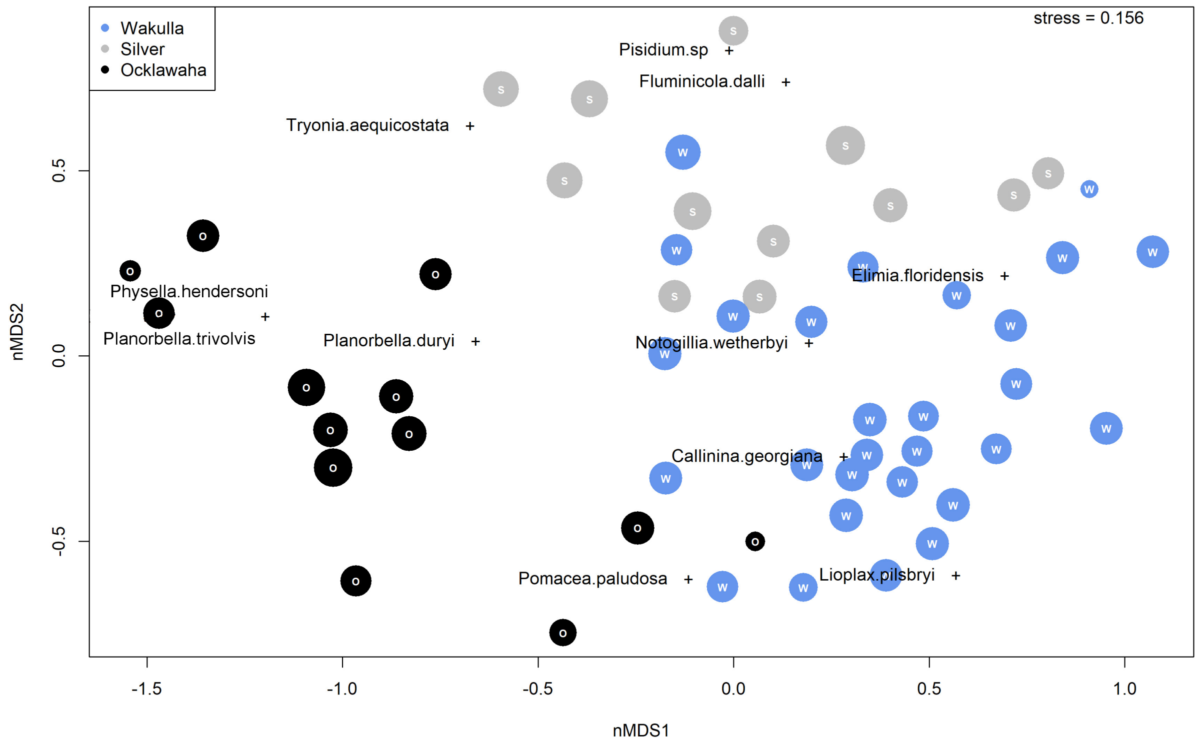

FIGURE 6 | Non-metric Multidimensional Scaling (nMDS) species and sample scores for fossil assemblages exclusively. Wakulla River samples in blue, Silver River samples in gray, and Ocklawaha River samples in black.

and Ocklawaha Rivers. This non-marine layer was interpreted as having formed in near-coastal, poorly drained marsh, pond, and stream paleoenvironments (Karrow et al., 1996). The third locality, the basal layer in the Leisey Shell Pits in Hillsborough County, contains dark, organic-rich sediment with freshwater and estuarine mollusk fossils of the middle Pleistocene Bermont Formation (Bogan and Portell, 1995; Portell et al., 1995). The site lies about 175 km SW of the sampled Silver and Ocklawaha River sites. Paleoenvironment is interpreted as having been a protected bay or lagoon fed by an adjoining large river, likely the source of the freshwater fossil material (Portell et al., 1995).

Compared to their fossil presence, most native, freshwater species saw a reduction in their modern geographic ranges with many undergoing local extirpation from the Silver, Ocklawaha, and Wakulla Rivers, though persisting within the broader region. Two prominent introduced, freshwater species (*C. fluminea* and *M. tuberculata*) were documented first appearing in the Florida Gulf and St. Johns River watershed between 1960 and 1973 (Heard, 1964; Schneider, 1967; Clench, 1969; Daniel et al., 2021). The euryhaline *V. usnea* has also been documented in the fossil record of Florida and nearby regions (Kittle and Portell, 2010; Czaja et al., 2019). A full listing and discussion of all species is available in **Table 2** and Supplemental Discussion ("Expanded Comparative Local and Regional Faunal Context").

DISCUSSION

Diverging Live Communities

Changes in the live communities of these rivers appear to reflect environmental and anthropogenically-related impacts to these fluvial ecosystems. In both river systems, the faunal composition of live mollusk associations has diverged from that observed in fossil assemblages, as demonstrated by statistically significant (**Table 3**) separation of live and fossil samples in the ordination space (**Figure 5**). These rivers have also become faunally dissimilar from one another through the differential loss of native freshwater species, the regionally variable spread of the introduced species *M. tuberculata* and *C. fluminea*, and encroachment of *V. usnea* into the coastally influenced lower Wakulla River. Whereas the decline in freshwater mollusk diversity was previously suggested based on fossils in Florida (Auffenberg et al., 2006), this study demonstrates that different river systems experienced diverging compositional shifts that resulted in increased faunal heterogeneity on a regional scale.

The compositional divergence in live communities of the two rivers is not solely a consequence of the modern presence of introduced species, but also represents changes in the remaining native, freshwater community. When introduced species are excluded, most live samples still separate by river system along nMDS2 (**Supplementary Figure 4**). Live samples also separate from fossil samples in the ordination space. As most of the species lost from modern assemblages were shared between the two river systems, divergence documented in live samples is likely caused by changes in the presence and relative abundance of the remaining native species. When introduced species are excluded, the freshwater communities of the two rivers are increasingly dominated by either *E. floridensis*, *N. wetherbyi*, or a combination of the two. In the Silver and Ocklawaha Rivers, *C. georgiana* also remains a notable component of the community at a relatively limited number of sites compared to the more widely dispersed *E. floridensis*.

In addition to invasive species, the native freshwater community may be responding to climate and anthropogenic factors including habitat loss, decreasing waterflow, excessive nutrient input, salinity fluctuations, and other impacts (Turner and Rabalais, 1991; Loper et al., 2005; Brainwood et al., 2006; Turner et al., 2006; Lysne et al., 2008; Liu et al., 2009; Heffernan et al., 2010; Donoghue, 2011; Bricker et al., 2014; Camp et al., 2014; Hong et al., 2014; Liebowitz et al., 2014; Freshwater Mollusk Conservation Society, 2016; Lauretta et al., 2019; Reaver et al., 2019). Invasive species (molluscan and non-molluscan) may directly or indirectly affect the native freshwater community through competition for resources, habitat alteration, or increased predation pressures (Isom, 1986; Leff et al., 1990; Wingard et al., 2008; Nico et al., 2009; United States Fish and Wildlife Service, 2014; Valentine-Darby et al., 2015; Ferreira-Rodriguez et al., 2016).

Fossil Community Composition

The composition of fossil communities provides a historical perspective to spring and river ecosystems critical for making informed restoration and conservation decisions. Fossil assemblages show similarity in faunal composition, despite the considerable distance (> 250 km) between the two studied river systems. Almost all fossil species present are shared between the two systems, with those absent from the Wakulla relatively rare in Silver/Ocklawaha samples. Given that radiocarbon dates on mollusk fossils coincide with the activation of spring flow across much of Florida (Balsillie and Donoghue, 2011; Donoghue, 2011; O'Donoughue, 2015; Kusnerik et al., 2020), the observed faunal resemblance of the two relatively distant river systems suggests that Florida springs and rivers were initially colonized by a similar suite of mollusks, reflected in the similarity of their fossil assemblages. Many fossil species identified in this survey have also been documented in freshwater fossil assemblages elsewhere in Florida (Karrow et al., 1996; Auffenberg et al., 2006), further suggesting that similar mollusk assemblages populated multiple Florida springs and rivers during the late Pleistocene-early Holocene.

Fossil samples from the Silver and upper Wakulla Rivers show a high degree of compositional fidelity, with many samples overlapping in ordination space (**Figures 5**, **6**) suggesting the headsprings and upper reaches of the two rivers hosted similar mollusk communities in the past. Species shared in relatively high abundances between the two regions include *E. floridensis*, *N. wetherbyi*, and *C. georgiana*, all endemic to the southeastern United States (**Figures 5**, **6**; Clench, 1962; Chambers, 1990; Thompson, 1999). Ocklawaha River samples form a more distinct cluster in the ordination space, perhaps because its fossil assemblages record more downstream communities rather than those of the headspring and upper river reaches. The interpretation of the Ocklawaha River samples as representing downstream mollusk associations, distinct from those of the headspring is further supported by their proximity in the ordination space (**Figures 5**, **6**) not only to fossil samples from the lower Silver River (as expected given their close geographic proximity), but also those of the lower Wakulla River. These Silver and Ocklawaha Rivers samples are similar in terms of comparably moderate proportional presence of *T. aequicostata* and *P. duryi*. Compositionally similar Ocklawaha and Wakulla Rivers samples share high relative abundances of *P. paludosa* and *C. georgiana*, perhaps reflecting a preference of both species for soft substrates and slower water flows than typically found in upstream or headspring environments (Duch, 1976; Katoh and Foltz, 1994).

Whereas the changes in assemblage diversity documented in this study (reduced live species richness, increased fossil beta diversity, etc.) may be attributed to temporal- and spatial-averaging of fossil samples, the magnitude of those changes make this explanation unlikely. Fossil assemblages reflect long-term accumulations of shell material formed through time-averaging and post-mortem transport (Eagar, 1978; Kusnerik et al., 2020). These patterns would inflate alpha diversity, with a more pronounced effect in downstream areas that receive post-mortem accumulations from upstream regions. This would also reduce beta diversity between sites, as greater spatial and temporal mixing would make sites appear more similar to one another. Whereas this explanation (temporal- and spatial-averaging of fossil samples) for the perceived patterns is possible, the effects of these biases is expected to be much less dramatic (Tomašových and Kidwell, 2009, 2010) than those observed in this study, suggesting the effects documented in this study should not be attributed primarily to time-averaging and post-mortem transport.

Conservation and Restoration Management Suggestions

Conservation managers should evaluate the benefits and feasibility of targeted conservation or reintroduction of critical, freshwater species. In particular, unionid mussels are a bellwether of environmental or ecological conditions in freshwater systems, being sensitive to changes in salinity, water chemistry, and other environmental factors (Williams et al., 2014). A robust, diverse mussel population in a system is often evidence of a healthy environment, while their loss indicates the opposite. Even if an ecosystem is restored, any loss of unionid mussels also sees the loss of related ecosystem services including enhanced water filtration, nutrient recycling and storage, and habitat and substrate modification (Vaughn, 2018). The fossil and death assemblages may provide critical information on past occurrences of unionid species, documenting their historical ranges and providing a context to where reintroduction may prove most successful (Haag and Williams, 2013).

Many freshwater species documented in this study were once present in these river systems, either historically or prehistorically, but are missing from the living record due to a local extirpation. As many of these mollusk species persist regionally, their return would bolster biodiversity in these river systems. Anthropogenic reintroductions of macroinvertebrate populations may improve restoration outcomes, particularly in systems suffering from depauperate local populations where self-recolonization is difficult (Jourdan et al., 2018). These efforts have already been documented at the Wakulla River, anthropogenic reintroduction of *P. paludosa* populations in the early-to-mid 2000 (Darby et al., 1997; Loper et al., 2005; Wakulla Springs Alliance, 2021). Fossil and death assemblage records may provide the most complete assessment of which species might be suitable targets for reintroduction, based on their previous occurrences in these freshwater systems.

Restoration, conservation, and reintroduction efforts will also benefit from ongoing efforts to reduce harmful environmental stressors. Impacts to Florida's freshwater systems are many and varied but notably include increasing withdrawal of groundwater, nutrient runoff and related harmful algal blooms, and human-induced changes in shore erosion and sedimentation rates (Florida Department of Environmental Protection, 2007, 2014). The negative impacts from these stressors degrade the environmental health of these systems, making them more susceptible to larger perturbations and decreasing the success of any reintroduction efforts (Jourdan et al., 2018). Continued monitoring of conditions in the springs, rivers, and adjacent terrestrial settings, as well maintaining many ongoing efforts to mitigate these effects, will enhance the long-term success of conservation and restoration efforts among freshwater faunal communities.

Finally, this study provides a historical perspective on the emerging ecological role of introduced species in spring-fed Florida rivers, thus emphasizing the importance of continued monitoring of those species and mitigating their impacts on freshwater systems. Florida has more non-native wildlife species than any other state (Hardin, 2007), and their effects on native populations and ecosystems should be monitored to prevent negative effects. Among introduced mollusks, *C. fluminea* populations must be maintained at low enough abundances to avoid negatively impacting populations of unionid mussels through competition for resources and overcrowding (Isom, 1986; Leff et al., 1990; Vaughn and Spooner, 2006; Ferreira-Rodriguez et al., 2016, 2018). Other introduced faunas may not directly compete for resources but cause negative impacts on native populations through habitat alteration, as in the burrows of the suckermouth armored catfish (Loricarridae) causing destructive shoreline erosion and sedimentation (Nico et al., 2009).

The impacts of invasive species mitigation must also be considered by conservation managers. Combating the spread of invasive aquatic plants such as *Hydrilla* has been an ongoing effort in many Florida freshwater environments, including Wakulla Springs. Unfortunately, more traditional removal methods such as mechanical harvesting has been documented to negatively impact native mollusk and other macroinvertebrate populations (Van Dyke, 2019). Alternative control methods, such as herbicide drip systems, reduced this impact but also highlighted the effects that some invasive species mitigation efforts have on other components of freshwater ecosystems (Van Dyke, 2019).

Effects of Sea-Level Changes

Rising sea levels in the Gulf of Mexico (Donoghue, 2011) leave the tidally influenced lower Wakulla River increasingly susceptible to increased salinization (Hong et al., 2014) and more vulnerable to storm surges from hurricane and storm events (Bromirski and Kossin, 2008; Knutson et al., 2019, 2020; Kossin et al., 2020). Storm surges and salinity disruptions like those documented in the modern Wakulla River are hypothesized to have previously caused the local loss of many freshwater taxa at the Page-Ladson site sometime after 9,950 cal BP, the youngest recorded deposits at the site, leading to the depauperate mollusk faunas of the modern Aucilla River (Auffenberg et al., 2006). In the lower Wakulla River, the mollusk community has been altered by the encroachment of saline waters, which displaced saline-intolerant native species that were replaced by taxa more tolerant of oligohaline conditions (Lewis et al., 2009; Hong et al., 2014).

The Value of State Parks

The upper Wakulla River may serve as a partial refugium for less saline-resilient freshwater species, as it is buffered from the effects of sea level rise and increasing salinity, and more protected from direct human impacts by the surrounding Edward Ball Wakulla Springs State Park. Numerous strategies for preserving the headspring and Wakulla River are being considered or implemented (Loper et al., 2005; Florida Department of Environmental Protection, 2007, 2020; Howard T. Odum Florida Springs Institute, 2014).

The Silver River has experienced substantial, protracted, anthropogenic impacts over at least two centuries. Although development of the springs as a tourist destination began as early as the 1820s, large changes between 1924 and 2013, including the addition of gas-powered glass bottom boat tours, exotic animal exhibits, a waterpark, and other attractions likely left lasting impacts on the aquatic communities of the headspring and river (Berson, 2011). In 2013, the Florida Park Service took control of property around the headspring, merging it with an existing, adjacent park to form Silver Springs State Park. With the addition of the headsprings, the Silver River and much of the Ocklawaha River now lie within a continuous stretch of State Park or state-managed lands, enabling more effective conservation efforts to address environmental challenges related to decreasing water flow, excessive nutrient runoff, and the impact of the Rodman/Kirkpatrick Dam on the Ocklawaha River and its tributaries (Shuman, 1995; Munch et al., 2006; Noll and Tegeder, 2011; Florida Department of Environmental Protection, 2014; Bi et al., 2019). Although no studies have documented how the recent incorporation of the headspring into the larger state park has impacted the aquatic communities, the removal of many of the attractions will likely reduce the direct anthropogenic impact on the river, possibly enabling recovery and restoration of the freshwater mollusk species that remain.

This study supports the importance of evaluating, maintaining, and expanding of the ongoing conservation and restoration strategies for Florida's freshwater spring and river ecosystems, including connection of protected lands/waterways, management of invasive species, and preservation of existing fluvial and riparian buffers (Castillo et al., 2016). The State Parks, and similarly managed lands, likely enhance the resilience and long-term diversity of freshwater habitats. Protection of these regions should be maintained and, if possible, enhanced through increased safeguards and expansion. The creation or expansion of managed areas around critical headspring regions can provide increased buffer zones, mitigating the impacts of harmful human or natural perturbations (De Freese, 1995). Expansion of these areas may also enhance connections between managed lands. These connections provide critical aquatic wildlife corridors, reducing habitat fragmentation and ensuring populations can move freely along and between waterways. Aquatic wildlife corridors and interconnected waterways are critical for population flow among fluvial species and may allow for natural recolonization following local extirpation events (Jourdan et al., 2018). Fluvial connections may also be restored through the removal of human-related impediments such as dams, artificially channeled rivers, and similar features which prevent freshwater species from accessing potential habitats. Reducing these barriers will become increasingly important, allowing populations to move within and between waterways, as available habitable space shrinks due to sea level rise, salinity fluctuations, pollutant perturbations, and other direct and indirect anthropogenic influences already affecting the springs and rivers in the region (Loper et al., 2005; Hong et al., 2014) and across other parts Florida (Walsh, 2001; Endries et al., 2009; White and Crisman, 2014).

Spatial, Temporal and Fossil Record Considerations

The results reported here should be considered in the context of the spatiotemporal resolution of the fossil record. While radiocarbon dating (Kusnerik et al., 2020) suggests that a continuous record of mollusk associations from the Pleistocene to today is absent from sample intervals, the presence of mid-to-late Holocene shells in death assemblages suggests these younger fossil deposits are present but less abundant than the more heavily sampled late Pleistocene-early Holocene deposits (Kusnerik et al., 2020).

Because of time-averaging, fluvial fossil samples are temporally mixed over hundreds to thousands of years, thereby combining specimens of dramatically different ages (Kusnerik et al., 2020). Pooling of live data from multiple seasons and years into a single sample, as was done in this study, mimics to some extent the time-averaging that characterizes fossil samples (Peterson, 1977; Martin et al., 2002). Additionally, the results reported here represent a regional case study and their broader applicability needs to be validated and refined in future studies in other river systems before this approach can be applied on larger geographic scales and in a more diverse array of habitats. For a more detailed discussion on resolution consideration, refer to Supplemental Discussion "Extended Spatial, Temporal, and Fossil Record Considerations."

SUMMARY

Analyses of live and fossil freshwater assemblages demonstrated that past mollusk associations were more diverse and more homogeneous in faunal composition, compared to depauperate and spatially heterogeneous mollusk associations that exist in Wakulla, Silver, and Ocklawaha Rivers today. This shift in composition reflects increasing presence of non-native species (especially *M. tuberculata* and *C. fluminea*), extirpation of many native freshwater species, fundamental changes in the relative abundance of surviving native taxa, and increasing salinity disruptions in coastally influenced regions of Florida rivers. The findings support strategies for mitigating these impacts through preservation and restoration of critical springs and rivers including: (1) expansion of protected zones such as State Parks and state-managed lands, (2) reintroduction and/or conservation of critical native species including *P. paludosa* and unionid mussels, (3) reduction of stressors including input of nutrient-laden runoff and groundwater withdrawals, and (4) evaluation of the impact of invasive species on native communities (Loper et al., 2005; Munch et al., 2006; Florida Department of Environmental Protection, 2007, 2014, 2020; Howard T. Odum Florida Springs Institute, 2014; Wetland Solutions Inc, 2014; Florida Department of Environmental Assessment and Restoration, 2015). The conservation paleobiology approach used in this study reinforces the importance of considering the long-term history of local ecosystems and highlights the utility of the fossil record in providing a historical perspective that extends farther than provided by most modern surveys or written records. Comparison of fossil and modern communities can provide a perspective that enables the recognition of long-term faunal changes in altered, imperiled, or at-risk ecosystems to provide guidance for restoration, conservation, and/or mitigation.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

AUTHOR CONTRIBUTIONS

KK and MK contributed to the study conception and design, involved in draft manuscript preparation. KK, MK, RP, GM, and RM conducted fieldwork and sample collection. KK, MM, and AK conducted laboratory processing and analysis. All authors reviewed the results, provided editorial feedback, and approved the final version of the manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2022.851499/full#supplementary-material

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