
AMPHIBIAN ASSEMBLAGES IN ISOLATED WETLANDS ARE PREDICTED BY INTERANNUAL VARIATION IN FISH OCCUPANCY: A CASE STUDY FROM FLORIDA, USA

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Abstract.—Fish influence amphibian community structure in wetlands through predation and other means, with many imperiled species such as Gopher Frogs (*Lithobates capito*) being vulnerable to fish predation. Most fish lack the adaptations to colonize new bodies of water that are hydrologically isolated, and the causes of such colonization events are poorly understood, so changing fish occupancy status in isolated bodies of water may not be considered in management. We documented changes in fish status in 46% of 13 isolated wetlands previously surveyed at a state park in southeastern Florida, USA, and hypothesized that fish status and landscape would affect amphibian biodiversity and assemblage structure in these wetlands. In July 2022, we surveyed wetlands that were previously censused in 2013 using funnel traps to encounter amphibians. Fish status had a strong effect on amphibian assemblage structure, but landscape did not. These results have implications for the conservation of imperiled fishless-wetland breeding amphibians. During high flood event years, wetlands may be colonized with fish, and these fish may be extirpated during drought years. Managers should consider fish status in wetlands to be dynamic and adjust monitoring and conservation efforts accordingly.

Key Words.—community ecology; fish predation; gopher frogs; landscape ecology; mosquitofish

INTRODUCTION

Fish are known to affect amphibian community structure and reduce species diversity (Bradford 1989; Skelly 1996; Hecnar and M'closkey 1997; Pilliod et al. 2010; Holbrook and Dorn 2016). Even small fish may consume parts of amphibians (Lawler et al. 1999) and impose top-down effects on wetland communities. Amphibians have multiple adaptations to evade or dissuade fish predation pressure. For example, poisonous secretions are a common defense mechanism that allow species such as Pickerel Frogs (*Lithobates palustris*) to coexist with fish (Holomuzki 1995). Alternatively, tadpoles may alter their activity and foraging behavior in the presence of fish (Wellborn 1996). Worldwide, many anurans have evolved alternate reproductive modes that are hypothesized to assist in predator avoidance, in part by truncating development time (Crump 2015). In the U.S., however, anuran reproductive modes are less diverse compared to those found in the tropics and many amphibian species likely rely on their dispersal abilities to arrive at fishless, hydrologically isolated bodies of water to facilitate predator avoidance.

Predator-vulnerable amphibians that typically breed in fishless habitats include several species of conservation concern in the U.S. In the Southeast,

Gopher Frogs (*L. capito*) and Tiger Salamanders (*Ambystoma tigrinum*) are imperiled in several states within their range, and both species are known to be negatively affected by fish (Gregoire and Gunzburger 2008; Maurer et al. 2014; Holbrook and Dorn 2016). Flatwoods salamanders (*A. bishopi* and *A. cingulatum*) are federally listed species that use isolated wetlands and larval survival may be reduced in the presence of fish, although support for this idea is limited (but see Gorman et al. 2009 and Mitchell 2021). In the western U.S., Mountain yellow-legged frogs (*Rana sierrae* and *R. mucosa*), as well as Cascades Frogs (*Rana cascadae*) are imperiled by the anthropogenic introduction of fish into heretofore fishless montane ponds (Pope et al. 2008; Bonham, C. 2011. A status review of the Mountain yellow-legged frog (*Rana sierrae* and *Rana muscosa*). California Department of Fish and Game. Available from: <https://nrm.dfg.ca.gov/documents/ContextDocs.aspx?cat=CESA-Listing> [Accessed 1 August 2025]).

Fish have limited ability to disperse to isolated wetlands and ponds, especially when compared to amphibians, primarily because they lack certain adaptations for traversing uplands such as legs or lungs. The absence of overland dispersal mechanisms in most native North American species, as well as a paucity of air-breathing or desiccation resistant traits,

means uplands represent a high resistance matrix to fish dispersal, and most fish are dependent on passive or opportunistic means of transport. Passive means of dispersal may include bird-borne zoochory (Lovas-Kiss et al. 2020) or fish rain (Hirsch et al. 2018) due to tornadoes or hurricanes, while opportunistic dispersal occurs during events such as flooding when temporary dispersal corridors may open to fish movement, perhaps only for minutes or hours. Additionally, in many regions anthropogenic stocking for sportfishing (Schilling et al. 2008) and mosquito control (Pyke 2008) is important. These mechanisms that allow fish to colonize new hydrologically isolated habitats have not been adequately studied or discussed (see Hirsch et al. 2018 for the most robust discussion currently published) and warrant more study to address the dominant hypotheses.

In at least some systems, flooding events are a primary driver of dispersal (Baber et al. 2002; Hohošova et al. 2010; Penha et al. 2017), especially in topographically homogenous regions in the U.S. such as the southeastern Coastal Plain, the Mississippi Valley, and the Prairie Potholes region. Flooding events may include predictable, yearly flooding in wet season/dry season habitats (Penha et al. 2017). Conversely, stochastic events such as hurricanes or other large storms may also cause previously isolated wetlands to be temporarily connected (McLean et al. 2016). Whether fish colonization occurs by either predictable or stochastic means can lead to a dynamic occupancy of fish in wetlands, thus these wetlands may act as critical habitat for imperiled amphibians in years when they are fishless or an ecological trap in years in which they are colonized by fish, reducing local wetland amphibian richness (Holbrook and Dorn 2016). Such changes are important for land managers to consider as the change in fish status may be more common than typically acknowledged. We offer the following case study of dynamic fish status in isolated wetlands in southeastern Florida as support for this contention and give our observations on the effects of fish status on amphibian assemblage structure.

We examined a subset of the isolated wetlands surveyed by Holbrook and Dorn (2016) to examine the hypothesis that fish occupancy and assemblage structure changes at wetlands, which then causes amphibian assemblage changes. We predicted that fish occupancy and richness would change at some of the sites through time. We also predicted that amphibian assemblages in isolated wetlands would be structured by local and landscape variables, with local variables

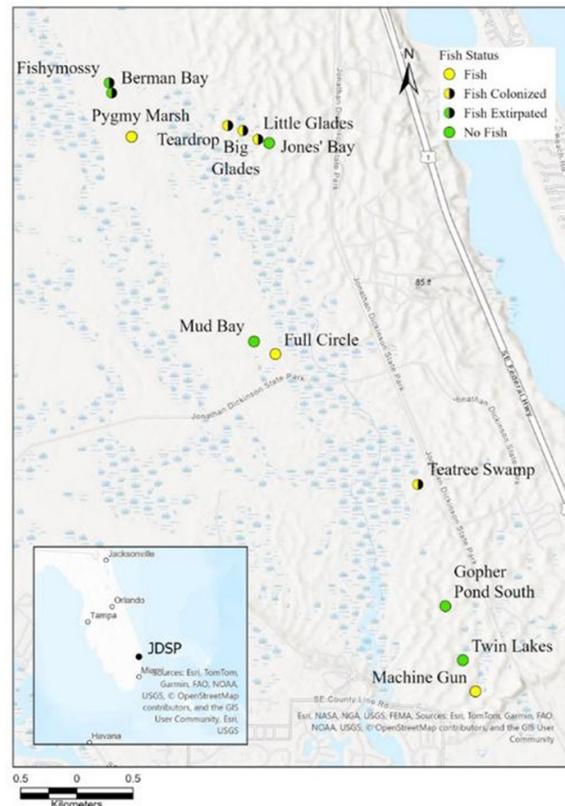


FIGURE 1. Map of isolated wetlands sampled in Jonathan Dickinson State Park (JDSP) in Martin and Palm Beach counties, Florida, USA. All wetlands originally sampled in 2013, except for Teardrop and Big Glades (reported as fishless in 2017 by Gonzales and Laughinghouse 2022). Sites marked Fish and No Fish had fish populations or were fishless across both sampling periods, respectively. Sites marked Fish Colonized were fishless in the first sampling period but had fish in 2022; sites marked Fish Extirpated had fish populations in 2013 or 2017, but none were detected in 2022.

(e.g., fish richness, fish presence) contributing more to assemblage structure than landscape variables (e.g., upland habitat, topography).

MATERIALS AND METHODS

Study site.—Jonathan Dickinson State Park (JDSP) is a 590-ha state park in Palm Beach and Martin Counties, Florida, USA (Fig. 1). Sandhill/scrub vegetative communities dominate the eastern portion of JDSP where most wetlands are isolated due to topography, while the western portion consists of Pine Flatwood Uplands and most wetlands are interconnected, although these pine flatwoods possess some isolated wetlands. The wet season trends in southern Florida produce seasonal flooding, typically beginning in June, which coincides with the reproductive peak for many amphibians and fish.



FIGURE 2. Select isolated wetlands and fauna from Jonathan Dickinson State Park, Martin and Palm Beach counties, Florida, USA. (a) Gopher Pond South, a long hydroperiod (mean 13.5 mo) isolated wetland that supports populations of Gopher Frogs (*Lithobates capito*) and was ostensibly fishless in 2013 and 2022. (b) Little Glades, a Sawgrass (*Cladium jamaicense*) dominated long hydroperiod (mean 16 mo) wetland that was ostensibly fishless in 2013 and was colonized with Everglades Pygmy Sunfish (*Elassoma evergladei*) by 2022. (c) A dragonfly (Aeshnidae) naiad predated upon an Everglades Pygmy Sunfish from Little Glades. (d) Twin Lakes, a permanent isolated pond that supports a Gopher Frog population and was ostensibly fishless in 2013 and 2022. (Photographed by Joshua Holbrook)

These seasonal floods create ephemeral (minutes or hours in length) connections between many heretofore isolated wetlands, which may allow colonization to new isolated wetland patches by fish. In addition, a large (> 10 cm in several hours) localized rain event in 2020 produced flooding beyond typical yearly fluctuations (pers. obs.). After this event all 10 isolated sandhill lakes censused during an opportunistic survey in the southeastern portion of JDSP in 2021 had resident Eastern Mosquitofish (*Gambusia holbrooki*) despite being previously fishless (unpubl. data). While these lakes were not included in this study, the ubiquitous presence of mosquitofish in isolated wetlands indicates a high connectivity rain event.

Holbrook and Dorn (2016) previously surveyed 20 wetlands at JDSP to quantify the fish and amphibian assemblage. We re-surveyed 11 of the wetlands (Fig. 2) that are typically hydrologically isolated (e.g., only connect overland to other bodies of water for minutes or hours during exceptional flooding events, but are otherwise surrounded by upland). These wetlands were interspersed throughout JDSP (Fig. 1) and previously consisted of both fishless and fish dominated habitats (Table 1). Additionally, we included two wetlands in JDSP that were reported fishless by Gonzales and Laughinghouse (2022) in

2017 for a total of 13 wetlands surveyed (Table 1).

Study design and sampling protocol.—Holbrook and Dorn (2016) sampled wetlands with a variety of funnel traps from June to November 2013 (<https://data.mendeley.com/datasets/ybysw55g7r/1>). In July 2022, we sampled all wetlands synchronously using 10 collapsible crayfish traps in each wetland (four Promar TR-503; Promar and Ahi USA, Gardena, California, USA; and six Ieasky crayfish traps, manufacturer information unknown). We placed the 10 traps per wetland on 19 July 2022 and checked and vacated traps each of the following three days (20–22 July 2022). We placed traps such that some of the traps in contact with the air to allow air-breathing organisms to survive. Based on the observations of Holbrook and Dorn (2016 in Appendix 1), three days of sampling is sufficient effort to document > 80% of fish species richness in our study wetlands. Additionally, the collapsible crayfish traps used in the current study had higher capture rates compared to the minnow traps (G-40 minnow trap; Tackle Factory, Fillmore, New York, USA) that were the primary trap type used by Holbrook and Dorn (2016).

We recorded captures and released all organisms from the traps after each check to minimize in-trap mortality. We also gathered local, landscape,

TABLE 1. Wetlands (n = 13) surveyed 15 June to 31 July 2013 and July 2022 with location (Latitude, Longitude), size (ha), fish species richness (S), amphibian S, hydroperiod, and distance to the nearest fish-containing wetland in 2022 (m), rounded to the nearest 5m. The top 6 wetlands had a change in fish status (extirpation or colonization). Wetlands marked with an asterisk (*) were reported fishless in 2017 by Gonzales and Laughinghouse (2022). Two wetlands recorded as fishless in 2017 (Teardrop, Big Glades) were not surveyed in 2013. Average hydroperiod in months for each site estimated by Holbrook (2014) based upon water gauge data from 2002–2012.

Wetland	Location	Size (ha)	Fish S 2013, 2022	Amphibian S 2013, 2022	Hydro-period (mo)	Distance to fish (m)
Fishymossy	27.0345, -80.1356	0.08	2, 0	0, 1	13.5	158
Berman Bay	27.0335, -80.1354	0.23	1, 0	2, 2	9.5	100
Teatree Swamp*	27.0015, -80.1107	0.8	0, 1	4, 1	7	58
Teardrop*	27.0311, -80.1262	0.47	0 (2017), 4	–, –	Permanent	45
Big Glades*	27.0312, -80.1249	2.92	0 (2017), 2	–, –	Permanent	45
Little Glades*	27.0303, -80.1242	1.25	0, 1	4, 4	16	30
Jones' Bay	27.0297, -80.1229	0.40	0, 0	5, 2	15.5	50
Mud Bay	27.0139, -80.1241	0.82	0, 0	4, 1	15.5	43
Full Circle	27.0130, -80.1225	3.18	5, 6	1, 1	12.5	20
Pygmy Marsh	27.0315, -80.1343	2.14	4, 1	4, 1	13.5	115
Gopher Pond S.*	26.9928, -80.1089	0.18	0, 0	5, 5	13.5	380
Twin Lakes*	26.9887, -80.1075	1.64	0, 0	5, 5	Permanent	70
Machine Gun	26.9865, -80.1059	6.24	5, 4	0, 0	Permanent	20

and time-based variables for each site (Table 2). Specifically, we gathered pH with a multiparameter meter (Hanna Instruments, Smithfield, Rhode Island, USA), determined wetland area using ArcGIS (Esri, Redlands, California, USA), and used previously published hydroperiod estimates for each wetland (Holbrook 2014; Table 1). We calculated terrain heterogeneity with a 100-m Vector Ruggedness Measure (Dilts et al. 2023) in ArcGIS, a measurement of landscape heterogeneity that calculates a value for a 100-m buffer around a point based upon slope, aspect, and elevation. We determined distance to nearest fish-containing wetland by first sampling nearby wetlands to determine fish status and then using ArcGIS to determine the distance of each of the study wetlands to its nearest fish-containing neighbor. We consulted published management data to determine upland habitat type (Gengenback 2012). We represented date by noting whether the sampling occurred in 2013 or 2022.

Data analysis.—Because sampling duration differed between 2013 and 2022, we used only the data from Holbrook and Dorn (2016) from 15 June to 31 July 2013 (e.g., during the period when the anuran species breeding would overlap with the 2022 sampling window and flood stage was similar) and expressed catch in both years as a percentage of the

whole catch for each species instead of a catch-per-unit-effort. Although the onset of wet season can lead to annual variation in breeding phenology in amphibians, overall species we encountered across all wetlands in July 2022 were similar to those encountered in June and July 2013, and both years had normal rainfall patterns (e.g., onset of wet season occurred with > 100% of average rainfall in June

TABLE 2. Local, landscape, and time-related variables hypothesized to affect amphibian assemblage composition in wetlands of southern Florida, USA, with collection method for each variable.

Variable Group	Variable	Method or measure
Local	Fish Presence/Absence	Collapsible Crayfish Traps
	Fish Richness	Collapsible Crayfish Traps
	Wetland Hydroperiod (months)	Months (Holbrook 2014)
	pH	Multiparameter Meter
	Wetland Size	ha; ArcGIS
Landscape	Habitat	Sandhill or Flatwoods (Gengenback 2012)
	Local elevational heterogeneity	ArcGIS, Vector Ruggedness Index
	Distance to fish-containing wetland	Collapsible crayfish traps or dipnets, ArcGIS
Time	Year	2013 or 2022

2013 and 2022; <https://www.sfwmd.gov/weather-radar/rainfall-historical/sites-and-basins>).

We evaluated the contribution of year, local, and landscape factors (Table 2) to amphibian assemblage structure in wetlands in 2013 and 2022 using Variation Partitioning. This analysis allows us to consider the relative effects of multiple measured processes on abundance data, as well as variation in abundance explained by multiple processes simultaneously (Logue et al. 2011). We analyzed these data using the vegan package (Oksanen et al. 2022) in R Statistical Software (R Core Team 2024).

RESULTS

Of the 13 wetlands sampled, 46% ($n = 6$) changed fish status from previous surveys. Fish were ostensibly extirpated at two wetlands and colonized four wetlands (Table 1). We encountered 10 species of fish, among which the Eastern Mosquitofish and Golden Topminnow (*Fundulus chrysotus*) had the highest occupancy (both 43%; Table 3). We also encountered eight species of amphibians, of which two were only encountered in fishless wetlands (Table 4), and one was only encountered in a fish-dominated wetland. Everglades Pygmy Sunfish (*Elassoma evergladei*) newly colonized one wetland (Little Glades) since 2013. Everglades Pygmy Sunfish are not known to predate upon amphibians, and Little Glades possessed Southern Cricket Frogs (*Acris gryllus*), Pinewoods Treefrogs (*Hyla femoralis*), and Barking Treefrogs (*H. gratiosa*). We otherwise encountered these three frog species exclusively in fishless wetlands. Fish generally reduced the mean number of amphibian species present ($S = 2.17 \pm$ [standard error] 0.6 versus $S = 3 \pm 0.77$ in wetlands without fish; Table 1).

The variation partitioning analysis indicated local variables primarily drove amphibian assemblage structure ($r^2 = 0.25$, $P = 0.046$), and time was marginally significant though its effect on assemblage was low ($P = 0.055$; Table 5). Landscape variables did not affect amphibian assemblage ($P = 0.364$), nor did the shared contribution of any variables (Table 5). A large amount of variation remained unaccounted for by any measured variable ($r^2 = 0.660$). Our sample size was limited because we had to omit three sites. We omitted Machine Gun (Table 1) from the community analysis results because we did not catch any amphibians in 2022. We also omitted census data from Big Glades and Teardrop in 2013, as these two were not sampled by Holbrook and Dorn (2016),

TABLE 3. Fish species encountered in July 2013 and July 2022 in Jonathan Dickinson State Park, Florida, USA. Percentage occupancy in fish-dominated wetlands, sorted by percentage occupancy in 2013.

Species	Occupancy 2013	Occupancy 2022
Eastern Mosquitofish (<i>Gambusia holbrooki</i>)	60%	43%
Everglades Pygmy Sunfish (<i>Elassoma evergladei</i>)	60%	29%
Golden Topminnow (<i>Fundulus chrysotus</i>)	60%	43%
Blue Spotted Sunfish (<i>Enneacanthus gloriosus</i>)	40%	14%
Warmouth (<i>Lepomis gulosus</i>)	40%	29%
Black Acara (<i>Cichlasoma bimaculatum</i>)	20%	14%
Bluegill (<i>Lepomis macrochirus</i>)	20%	14%
Dollar Sunfish (<i>L. marginatus</i>)	20%	0%
Largemouth Bass (<i>Micropterus salmoides</i>)	0%	14%
Walking Catfish (<i>Clarias batrachus</i>)	0%	29%
Yellow Bullhead (<i>Amerius natalis</i>)	0%	29%

but included census data for these sites for 2022. The lack of amphibian catch at Machine Gun is unsurprising because its fish species richness is high and includes large predators (e.g., Largemouth Bass, *Micropterus salmoides*, and Florida Gar, *Lepisosteus platyrhincus*), and this ponded wetland only produced two individual amphibian captures in 5 mo of field sampling in 2013 (Holbrook and Dorn 2016).

DISCUSSION

We document a dynamic geographically isolated wetland faunal community driven by fish colonization and sequential assemblage structure change in amphibians. Our study is one of the first to document such local fish extinction and recolonization events in isolated wetlands through time, although such metacommunity dynamics in fish are well documented in connected systems (e.g., riverine systems and lakes with aquatic connections; Bouvier et al. 2009; Penha et al. 2017; Vardakas et al. 2020). Although we cannot determine fish absence with certainty (MacKenzie et al. 2002), fish detection with traps in wetlands and ponds is high (Hamer and

TABLE 4. Amphibian species encountered in fishless and fish-dominated wetlands in Jonathan Dickinson State Park, Florida, USA, with percentage occupancy in wetlands surveyed. An asterisk (*) are for species only encountered at a fish-dominated wetland with Everglades Pygmy Sunfish (*Elassoma evergladei*), a species not known to predate upon amphibians.

Species	Occupancy Fishless	Occupancy Fish
Pinewoods Treefrog (<i>Hyla femoralis</i>)	100%	14%*
Barking Treefrog (<i>H. gratiosa</i>)	50%	14%*
Pig Frog (<i>L. gryllus</i>)	50%	71%
Gopher Frog (<i>Lithobates capito</i>)	33%	0%
Southern Leopard Frog (<i>L. sphenoccephalus</i>)	33%	14%
Southern Cricket Frog (<i>Acris gryllus</i>)	17%	14%*
Eastern Narrowmouth (<i>Gastrophryne carolinensis</i>)	17%	0%
Greater Siren (<i>Siren lacertina</i>)	0%	28%

Horányi 2024). For example, sampling by Holbrook and Dorn (2016) established fish status (fishless or fish-dominated) on the first day of sampling and did not change during 36 sampling days over 5 mo. Our work and others demonstrate the effect of fish on amphibian population abundance, diversity, and assemblage structure (Bradford 1989; Skelly 1996; Hecnar and M'closkey 1997; Pilliod et al. 2010; Holbrook and Dorn 2016). Collectively, these results highlight the metacommunity dynamics at play in isolated wetlands, which should be considered when addressing the conservation of pond-breeding amphibians.

Fish and amphibians in our study system, and likely many other landscapes, have differing barriers to dispersal that help explain the patterns we observed. Fish in Florida, and throughout the southeastern coastal plain, colonize new sites during landscape flooding events. In southern Florida especially, a strong wet season allows many of the wetlands on the landscape to be colonized during rain events in June and July (Baber et al. 2002; Goss et al. 2014). Once fish move to new patches, they change local faunal structure through top-down mechanisms such as predation and more generally, by creating a landscape of fear (Laundré et al. 2010). Amphibians, conversely, are not relegated to flood conditions to facilitate their dispersal, although most species make extended movements with rain events to avoid

TABLE 5. Results of variation partitioning, giving the contribution of local, landscape, and time variables, as well as the shared contribution of all groupings, to amphibian metacommunity assemblage structure in 13 isolated wetlands in 2013 and 2022 in southern Florida, USA. Specific variables for each variable group given in Table 1.

Variable	r^2	P -value
Local	0.25	0.04
Landscape	0.08	0.36
Year	0.09	0.06
Local + Landscape	0.003	–
Local + Year	-0.01	–
Landscape + Year	-0.08	–
Local + Landscape + Year	-0.01	–

desiccation. Once amphibians arrive in a patch, they are subject to local biotic conditions, including the presence of predatory fish.

Landscape variables had no apparent effect on amphibian assemblage structure in our study. In one sense this is unsurprising because the dispersal aptitude of amphibians; landscape heterogeneity or habitat type do not represent significant barriers to amphibians migrating through uplands to breeding sites. In another sense, though, if fish colonization affects amphibians and fish colonization is influenced by landscape heterogeneity (e.g., flat landscapes are more traversable to fish during flood events), then landscape should have an indirect effect on amphibian assemblage structure. It is possible that our landscape heterogeneity metric (vector ruggedness measure, VRM), however, may not have sufficient resolution to represent the flooding patterns that dictate fish movements within this relatively flat landscape. Finally, our sample size of fish-dominated wetlands included sites with the invasive Walking Catfish (*Clarias batrachus*), a species present in fewer wetlands in the 2013 sampling than in 2022. Walking Catfish can move overland and are thus less affected by landscape limitations. We excluded one notable variable, hydroperiod, from our local variables. Although hydroperiod may be an important variable to consider in some systems, previous work by Holbrook and Dorn (2016) in the system explicitly examined hydroperiod and found no effect on amphibian assemblage composition.

Given the dynamic nature of fish occupancy on the landscape, and the effect of fish on amphibians, management of isolated wetlands must be equally dynamic. This is especially true when considering management for imperiled amphibians whose breeding wetlands may change fish occupancy.

For example, Gopher Frogs are a species that often require fishless conditions for larvae to reach adulthood (Gregoire and Gunzburger 2008), and fish are hypothesized to impact flatwoods salamanders (Gorman et al. 2009). Gopher Frogs were only encountered in fishless wetlands in this study as well as in previous work in the region (Holbrook and Dorn 2016), in which all six wetlands with Gopher Frog tadpoles were fishless. Because of these and similar observations, much focus is rightly put upon individual fishless and long-hydroperiod breeding wetlands as Gopher Frog habitat.

It would be a mistake, however, to assume that all Gopher Frog breeding wetlands are static with respect to fish occupancy, because flooding may convert a breeding wetland into an ecological trap, a process that has previously been demonstrated with dragonflies (Odonata: Anisoptera) that colonize fish-dominated ponds (Šigutová et al. 2015), although it is unknown whether Gopher Frogs are able to detect fish kairomones (interspecific chemical signals) and avoid wetlands containing fish, thus avoiding the potential ecological trap. One of our sites (Teatree Swamp) that was fishless and had Gopher Frog tadpoles during previous work (Holbrook and Dorn 2016) contained fish during 2022 and we detected no Gopher Frog tadpoles. Given the limitations of our sampling, though, and the low detection probability of larval amphibians in some cases (Hamer and Horányi 2024) we cannot rule out the possibility that some small number of Gopher Frog tadpoles were present but went undetected.

Flooding may introduce fish to wetlands, but conversely, drought years may extirpate fish and expand the number of viable breeding wetlands for some species, even though such wetlands may not be subjected to monitoring or special protection. Drought has been demonstrated to have negative effects on amphibian breeding during the concurrent habitat reduction (i.e., wetlands drying) but may lead to population recovery through higher breeding success following such events (Moss et al. 2021; McDevitt-Galles et al. 2022). There is also evidence of reduced severity of chytrid infections following drought (Terrell et al. 2014), which may be connected to reduced stress levels from fewer predators, although we are unaware of whether this hypothesis has been explicitly tested elsewhere.

Wetland restoration and construction should also consider landscape flooding if the goal is to promote higher amphibian richness or support imperiled species sensitive to fish predation. Landscape

positions above the highest likely flood stage or farther from fish-dominated wetlands may be preferable in restorations targeting amphibians. It is especially important when considering the functional proximity of habitats with larger predatory species. Although it has been very poorly studied, different fish species undoubtedly have varying effects on amphibian assemblage, perhaps based on gape limitations (Bransky and Dorn 2013) or foraging strategy. Additionally, some closely related species such as sunfish (Centrarchidae) have been demonstrated to have differing resistance to amphibian poisons (Holomuzki 1995). In our study area, one wetland (Little Glades) was colonized by Everglades Pygmy Sunfish and no other species, yet this site remained more similar in composition to the fishless wetlands. Additionally, in the work of Holbrook and Dorn (2016), the 20 wetlands surveyed had amphibian compositional clusters apparently based on fish species composition, thus attention to the potential colonizer pool of local wetlands may be important.

Finally, the introduction of fish with unique abilities to traverse uplands is concerning for conservation purposes. Anurans in much of North America evolved in a landscape where fishless wetlands were present and accessible, and already many of these wetlands are being eliminated through climate change derived flooding, which may introduce fish, or profound droughts that may limit species due to development time restrictions (Ryan et al. 2014). Invasive fish species such as the Walking Catfish that can move over dry land are novel to most of the North American landscape and many amphibians lack predator resistance or avoidance mechanisms that are prevalent in areas with such fish. Such traits include a high diversity of reproductive modes (Crump 2015), which allow anurans to reproduce in shorter hydroperiod habitats and perhaps emerge prior to predator arrival. Other invasive fish with unique traits such as Asian swamp eels (*Monopterus* sp.), which can change sex and ostensibly aestivate in short hydroperiod wetlands (Pintar et al. 2024), have precipitated declines and small-scale extirpations of fishes and amphibian species in southern Florida (Pintar et al. 2023; Howell 2023.) Management strategies should seek to prevent invasion or control invasive fish with such adaptations for the sake of local amphibian biodiversity.

Fish status in many habitats worldwide is dynamic, and robust consideration of this fact has so far evaded the amphibian conservation and ecology literature. Fish invasion may be a primary determinant of

amphibian biodiversity and productivity, and most of the imperiled pond-breeding amphibians in North America lack fish resistant traits (Pope et al. 2008; Gregoire and Gunzburger 2008; Bonham, *op. cit.*; Maurer et al. 2014; Buxton and Sperry 2017). As climate change brings the twin effects of larger rain events, which allow for increased fish colonization, and prolonged drought, which may facilitate fish extirpation from local wetlands, the implications of such events should not be ignored by managers, ecologists, and conservationists.

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