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Evaluating the Ecological Importance of Seasonal Marshes as Breeding Habitats for Native Amphibians

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Abstract: Seasonal marshes, which fill in during wet seasons and are dry during part of the year, are important breeding grounds for many native amphibians. They are not as well protected as permanent water bodies because of their small size, variable water regime, and for the many of them not being inventoried by wetland lists. The present study examines the ecological value of seasonal wetlands as breeding habitat for amphibians using a well-structured narrative synthesis of 12 peer-reviewed studies that investigated the importance of temporary wetlands, pond-breeding amphibians and wetland connectivity. Evidence was grouped into six habitat dimensions: hydroperiod, pond area, predator regime, pond clustering and connectivity, surrounding terrestrial habitat and species interactions. The synthesis demonstrates that hydroperiod is the key factor regulating breeding success: drying occurs before metamorphosis leads to reproductive failure, while permanent water brings in fish which exclude sensitive species. Larval density and richness were greatest in fishless wetlands of intermediate size, while the number of neighbouring ponds and the amount of nearby forest affected colonisation and extinction and larval density. The number of species was found to vary for different combinations of habitat traits so that a variety of hydroperiods within a landscape will result in a higher diversity of amphibians than a single wetland type. Replacements often did not achieve amphibian goals, and the reduction in hydroperiods due to climate change became a problem. Two summary tables are provided to relate habitat attributes to amphibian responses and conservation challenges with management responses. Findings support protection of wetland networks, rather than individual sites, and hydroperiod diverse management and monitoring of wetlands with multiple metrics over time. The evidence is mainly limited to the temperate North America and therefore needs to be localized prior to extrapolation to monsoonal and tropical seasonal marshes.

Keywords: Seasonal Marshes; Temporary Wetlands; Vernal Pools; Pond-Breeding Amphibians; Hydroperiod; Wetland Conservation.

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I. Introduction

Seasonal marshes are shallow vegetated depressions that fill with water during wetter times of the year, but are dry for part of the year. Very similar systems have been described in the scientific literature by multiple names such as vernal pools, temporary ponds, ephemeral wetlands or seasonal ponds. The designation of seasonal marshes here is an umbrella term for wetlands that have a wet/dry cycle. These wetlands are ecologically different because they are often dry, and this leads to the presence of very specialised plant and animal communities including many species which are rare; these small water features also provide biodiversity, biogeochemical and hydrological functions to the landscape in which they occur (Calhoun et al., 2017).

This is an important property for the most dependent groups, such as amphibians. For the majority of native inhabitants of ponds, there are two different life stages – those in water as eggs and larvae, and those in terrestrial habitat as young and adults. It is, therefore, necessary for the wetland to provide a wet habitat for long enough to allow the larvae to metamorphose but to dry out often enough to prevent fish and other long-lived fish predators from inhabiting the wetland. Wetlands that satisfy both requirements are not common and are hard to detect as they are small and only occur for short periods in time. In many areas the numbers of amphibians have been declining and the importance of different breeding habitats is of conservation concern.

Protection of the seasonal marshes has also been compromised due to their classification. Wetlands that are surrounded by uplands are often considered geographically isolated, but they exchange water, materials,

energy, and organisms with other landscape features and play a role in flow generation, nutrient and sediment retention, and support of biodiversity, although legal protection has been weak even though these wetlands are preferentially lost (Cohen et al., 2016). The isolation label has been criticized since it hides hydrological and ecological disparity among the types of wetlands and suggests a level of separation that is not always accurate (Mushet et al., 2015). The assumption of isolation can result in systematic underestimation of the value of small seasonal wetlands for amphibians which shift between wetlands and uplands at various life stages.

This volume of site-level research is scattered across studies that vary by region, species and measured response, making it difficult to synthesize evidence of the amphibian breeding habitat function of seasonal marshes. This paper gathers all that evidence. It aims to (i) determine the habitat features that most influence the breeding success of amphibians in seasonal marshes, (ii) connect responses to the habitat features with those to the species and landscape level, and (iii) apply results to conservation and management priorities. The remainder of the paper presents a literature review, the synthesis methods, the results, a discussion of implications and a conclusion.

II. Literature Review

Pond size, Hydroperiod and Predators

Pond size is closely correlated with hydroperiod and predator regime, which in turn affects the ability to successfully breed amphibians. To determine if the density, richness and diversity of amphibian species changed with pond size, a survey of approximately 200 pounds over a 7,140-ha landscape in the Midwestern United States was conducted to test this hypothesis, and a quadratic model was found to be a better model than a linear model in each case, with the highest values at intermediate pond sizes (Semlitsch et al., 2015). The probability of drying is high for small ponds, while high fish colonization and accumulation of invertebrate predators are a result of predation in large ponds, which creates the peak. Fishless ponds of intermediate size were most diverse and yielded the highest numbers of larvae, and hylid and chorus frogs were more common in ephemeral ponds, while bullfrogs, green frogs and cricket frogs were more common in permanent ponds with fish.

Landscape Configuration and Habitat Structure

In addition to single wetlands, the distribution of ponds throughout a landscape affects amphibian communities. Larval density of the three species studied was strongly influenced by surrounding forest habitat, canopy cover, number of ponds within 300 m of a focal pond, presence of fish, basin slope, hydroperiod, and pond vegetation while surveyed; with the most important factors varying among species (Peterman et al., 2014). This species-specific pattern suggests a diversity of pond conditions required to maintain diversity.

A survey of 192 ponds on a landscape took a different tack. Larval density was best predicted by habitat features, while larval body size was most well explained by interactions among species, where larval density of a focal species was positively related to the density of congeners, and negatively related to the body size of congeners (Ousterhout et al., 2015). This discrepancy indicates that density may not be a valid measure of habitat quality.

Drought, Life History and Breeding Phenology

There is a further layer of temporal (time) variability. A multi-year study was conducted on two pond-breeding salamanders that have different breeding seasons, one spring and one fall; the results are shown below: A single year of drought resulted in high reproductive failure in the spring breeder (34% of ponds) while the fall breeder experienced cumulative failure over two years (8% of ponds available to the fall breeder decreased due to drying or failure to refill) (Anderson et al., 2015). Colonisation and extinction probabilities for both species were influenced by pond clustering, hydroperiod, forest cover and canopy

cover, indicating that the two species differ in their susceptibility to drought due to life-history variation. Interactions within the pond can also be influenced by the timing of breeding. Phenological differences between sympatric salamanders are important in the recruitment of the metamorphs and demographic patterns, with breeding phenology influencing larval size structure, and early breeding species potentially predating on later breeding species (Anderson et al., 2015). Together, the reviewed studies suggest that these factors (hydroperiod, predators, landscape configuration, and phenology) are all interrelated, with few studies integrating these factors in an evaluation of seasonal marshes as a breeding habitat. There is a motivation for the synthesis presented in the following sections due to this gap.

III. Materials and Methods

Review Design

Given the variability in species, region and study design and the variable response variables across the available studies, a structured narrative synthesis was used. The synthesis sought to determine if there were patterns in the relationship between habitat attributes of seasonal marshes and amphibian breeding outcomes and to the conservation of these wetlands.

Source Selection

Scholarly indexing services were used to identify peer-reviewed articles with combinations of the terms vernal pool, temporary wetland, ephemeral wetland, pond-breeding amphibians, and hydroperiod and wetland connectivity. Four criteria were used to determine whether to retain a source: (i) published in a peer-reviewed journal with a digital object identifier; (ii) published in a period of the past 10 years (2014–2022); (iii) included in the focus of the paper related to temporary or seasonal wetlands, pond-breeding amphibian ecology or wetland connectivity and conservation; and (iv) reported empirical, modelling, or review evidence relevant to breeding habitat. Preprints and non-peer reviewed reports were not included. A total of twelve sources from 2014 to 2020 were kept.

Analytical Framework

The sources were consulted for data regarding six habitat dimensions: hydroperiod, pond area, predator regime, pond clustering and connectivity, surrounding terrestrial habitat, and species interactions. Qualitative assessments of the direction of the reported amphibian response (positive, negative, peaked, or species-dependent) were made along with the study design. Results were then categorized into amphibian responses (Table 1) and conservation challenges with corresponding management responses (Table 2). No effect sizes were combined.

Limitations of the Approach

The corpus is small and was assembled by structured selection rather than by an exhaustive systematic search, so relevant studies may have been missed. Most retained field studies were conducted in temperate North America, and publication bias toward significant results cannot be excluded. Conclusions are therefore stated as patterns in the evidence rather than as quantitative effects.

IV. Results

Composition of the Evidence Base

The 12 retained sources included six field-based studies (landscape surveys, multi-year occupancy monitoring or metacommunity modelling), one hydrologic hindcast modeling study, and five reviews or syntheses on temporary wetlands, wetland connectivity, pool creation and amphibian dispersal. Field studies focused on the Midwestern and south-eastern United States, and included a higher frequency of salamanders than frogs. The reviews were extended geographically and gave context to the conservation.

Habitat Attributes and Amphibian Responses

The six habitat dimensions are summarized in table 1. Hydroperiod, a measure of the length of time the wetland remains waterlogged, was the single most consistent constraint on breeding success and has both positive and negative sides: a wetland that dries too early is inhospitable to metamorphosis, while a wetland that stays too wet admits fish. Pond area gave a peaked response as expected from this 2-way constraint, as the area is closely related to drying risk and predator accumulation. The strongest filtering effect was the predator regime. In ponds where fishes occurred many sensitive species (especially salamander) were missing, and generalist frogs remained in permanent ponds. Pond clustering and surrounding forest were repeatedly shown to be influential, but the direction and intensity of effects varied by species, for larval density and for colonisation and extinction. Body size and recruitment were more strongly influenced by species interactions and breeding phenology than by density; the choice of metric used for monitoring influenced the resulting conclusion about habitat quality.

Table 1: Habitat Attributes of Seasonal Marshes and Associated Amphibian Breeding Responses

Habitat attribute	Reported amphibian response	Evidence base	Pattern in evidence
Hydroperiod length	Drying before metamorphosis causes reproductive failure; permanent water admits fish and other predators that exclude sensitive species	Multi-year occupancy studies; hydrologic hindcast model; landscape surveys	Consistent; optimum differs by species
Pond area	Larval density, richness and diversity are highest at intermediate sizes; small ponds dry early and large ponds accumulate predators	Landscape survey of about 200 ponds	Peaked (intermediate size)
Predator regime (fish)	Fishless ponds produce more larvae; fish presence lowers colonisation by sensitive species, while generalist frogs persist with fish	Landscape surveys; metacommunity occupancy model	Negative for sensitive species
Pond clustering and connectivity	Number of nearby ponds is linked to larval density and to colonisation and extinction probabilities	Survey of 169 ponds; multi-year occupancy study	Influential for persistence
Surrounding forest and canopy cover	Forest and canopy cover relate to larval density and to occupancy dynamics of pool-breeding salamanders	Survey of 169 ponds; multi-year occupancy study	Influential; varies by species
Species interactions and phenology	Habitat predicts larval density, whereas interactions among species better explain body size; breeding timing shapes predation and recruitment	Survey of 192 ponds; field study of two sympatric salamanders	Trait-specific

Conservation Challenges and Management Responses

Table 2 correlates key conservation issues with responses to conservation identified through the evidence. There are two major difficulties. The first is an administrative one, small and seasonal wetlands are under-inventoried, and are often classified as isolated, reducing their protection. The second is ecological, in that replacement pools are not a reliable match for the hydrology and surrounding habitat of

natural seasonal marshes. Protection of wetland networks and adjacent terrestrial habitats, maintaining a variety of hydroperiods, and monitoring using more than one response metric were the top three responses with the most support in the evidence.

Table 2: Conservation Challenges for Seasonal Marshes and Corresponding Management Responses

Conservation challenge	Ecological consequence	Management response
Small size and incomplete inventories	Wetlands are missing from planning and maps, so cumulative loss goes unrecorded	Field inventories that record hydroperiod class; inclusion of small wetlands in regional plans
Weak protection linked to the isolation label	Wetlands surrounded by uplands lose protection despite hydrological and biological connections	Classification by function, for example hydrogeomorphic class, rather than by surface-water isolation
Shortened hydroperiods under climate variability	Fewer years are suitable for larval development; reproductive failure in drought years	Retention of wetlands with a range of hydroperiods, including longer-hydroperiod refuges; hydrology monitoring
Loss of pond clusters and terrestrial habitat	Reduced colonisation and movement among wetlands; weaker persistence	Protection of wetland networks together with surrounding forest and dispersal routes
Reliance on constructed replacement pools	Created pools often fail to support amphibian objectives	Creation as a last resort; adaptive management; monitoring for at least five years
Single-metric monitoring	Density alone can misrepresent habitat quality	Joint monitoring of occupancy, larval density, body size and metamorph recruitment

V. Discussion

Hydroperiod Diversity as an Organizing Principle

The synthesis suggests that the diversity of hydroperiod is, in fact, the organizing principle used to conserve amphibians in seasonal marshes, rather than the presence of one wetland type that is optimal for the conservation of amphibians. In a Florida wildlife refuge, it's illustrated through metacommunity modelling. The ornate chorus frog, an ephemeral wetlands specialist, exhibited greater persistence and colonisation in the short-duration wetlands while the most water-sensitive species, the mole salamander, was non-existent in short-duration wetlands and had the lowest persistence during drought. Another extreme condition that was detrimental was extremely wet, where the fishes were able to invade isolated wetlands, and then not the mole salamanders (Davis et al., 2017). For this reason, no one hydroperiod benefits all the species, and having a landscape with short, intermediate and longer duration wetlands protects amphibian communities from both dry and wet extremes.

Climate Variability and the Shortening of Hydroperiods

The impact of rainfall and evaporation on the hydroperiod is direct and directly affects breeding outcomes because larvae require a certain hydroperiod to complete development. Hindcast modelling of 17 breeding wetlands used by the reticulated flatwoods salamander (Ambystoma bishopi), a species requiring at least 11 weeks to metamorphose, identified only 61% of years in the last 120 years (from 1896 to 2014) that were favorable for the development of its larvae based on a conservative 12-week requirement, and that long-term mean hydroperiods were shorter than in any other year since 1896 (Chandler et al., 2016). The study is about one species in one region, but the mechanism is general; any decrease in the number of

years of a long enough wet phase reduces the successful reproduction frequencies. Seasonal marshes in areas where the rainfall is strongly seasonal and is likely to be sustained for periods of the year may also be vulnerable, although thresholds would have to be set locally. The impact of rainfall and evaporation on the hydroperiod is direct and directly affects breeding outcomes because larvae require a certain hydroperiod to complete development. Hindcast modelling of 17 breeding wetlands used by the reticulated flatwoods salamander (Ambystoma bishopi), a species requiring at least 11 weeks to metamorphose, identified only 61% of years in the last 120 years (from 1896 to 2014) that were favorable for the development of its larvae based on a conservative 12-week requirement, and that long-term mean hydroperiods were shorter than in any other year since 1896 (Chandler et al., 2016). The study is about one species in one region, but the mechanism is general; any decrease in the number of years of a long enough wet phase reduces the successful reproduction frequencies. Seasonal marshes in areas where the rainfall is strongly seasonal and is likely to be sustained for periods of the year may also be vulnerable, although thresholds would have to be set locally.

Connectivity, Dispersal and Landscape-Scale Protection

The influence of pond clustering on colonisation and extinction links local wetlands to landscape processes. Dispersal has been defined as a series of emigration, immigration and transience that is determined by the individual state and environmental context and affects both the demography and the genetics of populations (Cayuela et al., 2020). It is logical that recolonisation following a failed breeding season would be dependent on the availability of other wetlands at close range and terrestrial habitat that allows for movement. This interpretation reinforces the arguments for the classification and protection of wetlands based on relationships between wetlands, and helps to counter any tendency to view small wetlands with uplands around them as "disposable".

Management Implications and the Limits of Pool Creation

The management implications are congruent throughout the evidence. Current seasonal marshes should be mapped and managed as systems that include adjacent forests, and where possible, efforts should be taken to preserve a variety of hydroperiods. A review of the creation of pools in north-eastern and central North America has found that created pools do not necessarily support amphibian goals, require adaptive management and monitoring for at least five years, and are a last resort option when natural pools can no longer be preserved (Calhoun et al., 2014). The status survey of man-made ponds (Section 2.2) indicates that such ponds can also be a valuable reproductive resource, but primarily when a diversity of hydroperiods and basin slopes are present, a design consideration not an excuse to displace a natural wetland. Designing for monitoring should be considered. As density and body size were different driving factors, programmes that only record density may overestimate habitat quality. Managerial decisions would be better justified with joint occupancy, density, body size and metamorph recruitment, and measurement of hydroperiod.

Limitations and Research Needs

There are three limitations to the conclusions. First, the evidence base is limited, and they have been assembled by a structured selection process and should not be interpreted as a complete evidence base. Second, thresholds like the intermediate pond size optimum or the importance of neighbouring ponds within a few hundred metres are not necessarily true for monsoonal or tropical seasonal marshes, since there is little field evidence to support these limits in these regions. Third, no new field data were collected. Additional needs for the region include long-term hydrologic records at breeding wetlands, region-wide surveys of frogs and salamanders along hydroperiod gradients, and studies of the maintenance of dispersal in wetland networks with shorter wet seasons.

VI. Conclusion

The alternating wet and dry conditions of seasonal marshes provide important breeding habitat for native amphibians, since the wet conditions enable the development of larvae and the dry conditions enable many aquatic predators to be excluded. Analysis of 12 peer-reviewed studies reveals that hydroperiod is the most important factor affecting breeding success, fishless wetlands of intermediate size tend to have the highest larval densities and richness, and neighbouring ponds and surrounding forest affect colonisation and persistence. Conservation outcomes improve in a landscape with wetlands of a variety of hydroperiods, due to the different hydroperiod tolerances of species. Hydrologic hindcasting suggests that a decrease in wet season length will result in fewer years for larval development and further stresses the need to preserve existing wetlands. Replacement pools are often found to be inadequate in providing habitat and should be used as a last resort. The next four priorities are inventory and classify small, seasonal wetlands by their functions rather than their apparent isolation; protect wetland networks coupled with their terrestrial neighbors; maintain variety of hydroperiods; and monitor multiple response metrics for at least five years. The main constraint is that of a limited number of studies available for temperate North America, and the need to conduct field studies in other regions prior to threshold determinations for monsoonal and tropical seasonal marsh ecosystems. In this context, the evidence indicates that seasonal marshes should not be considered a marginal or expendable wetland, but should be included as part of an amphibian conservation programme in this system.

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