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Habitat Specialization and Community Turnover among Aquatic Beetles in Temporary Ponds

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Abstract: The temporary ponds form, decrease in size, and disappear according to a pattern dictated by rainfalls and droughts; yet, there is an aquatic beetle assemblage that persists through wet and dry periods in the pond. In this paper, we examine how the processes of habitat specialization and community turnover are involved in the process of persistence of these assemblages. The reason why beetles are chosen as the main objects of study is that they have flight dispersal capabilities as well as drought-resistant life stages, and therefore, they can help understand how assemblages are reconstituted every year. Instead of conducting one field research, we provide a map of evidence based on twelve recent scientific articles on invertebrates, amphibians, spiders, bees, and whole-biota freshwater studies, and then we interpret these results in terms of beetle-based study. There were five main topics of coding for each source: habitat specialization, community turnover, hydroperiod and seasonality, human-made or managed water bodies, and predation. None of these sources considered the two concepts concurrently, and none had beetles as the focus of study. Based on this trend, it may be possible to outline a four-step process in which drying serves as a sieve, specialists and generalists react to each other differently, dispersal helps restore community structure following rewetting, and management and predators alter the process. This model leads to the formation of four hypotheses, one of which is that specialists will be present in stable ponds whereas generalists will cause turnover in ephemeral ponds. It is suggested that constructed and restored ponds may provide habitat for temporary water beetles provided that hydroperiod diversity is conserved.

Keywords: Temporary Ponds; Aquatic Beetles; Habitat Specialization; Community Turnover; Hydroperiod; Metacommunity; Pond Management.

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I. Short-Lived Waters, Long-Lived Questions

In any map of a lowland landscape, there will be no difficulty in locating the permanent lakes, but not so for the temporary ponds. The latter depend on rain or snow for filling up, they retain water for weeks or even months before they get dried up into cracks on the muddy ground. As such, they are usually overlooked in the listing and management plans because they do not contain much life, except when they were full with water. However, research on the communities of macroinvertebrates living in tropical temporary ponds has shown that temporality influences the functional traits in the communities in ways that are dependent on the duration and season of the wet period (Tette-Pomárico et al., 2023). Aquatic beetles are a natural group of organisms to focus on here.

Two concepts may provide explanations to such assemblages. The first one is habitat specialization. Specialists react differently to the danger compared to generalists. Habitat specialization was used as a cue of choosing habitat when the top predator was present in an experiment (Šigutová et al., 2021). Another concept is community turnover, which means the substitution of species among ponds and during a certain period of time. Community turnover is the feature of metacommunity, where local communities interact due to the process of dispersal. The small-bodied meiofauna species have been considered as a model to test the above-mentioned concepts (Minot et al., 2021). The authors questioned what causes the functionality of the species – the species turnover or traits' differences between species (Gansfort et al., 2020). This question can be also asked about beetles.

Thirdly, many ponds today are artificial ponds. Artificial ponds have been considered a good source of habitat for aquatic insects in southern Africa, which is known for its drought-prone environment (Samways et al., 2020). Dragonfly and damselfly populations have been studied in relation to colonization of the

artificial ponds in the past to understand how communities evolve (Minot et al., 2021). For effective management of beetles together with artificial ponds, it needs to be determined if the water sources create specialist, generalist, or both types of beetles.

This paper attempts to establish the connection between specialization and turnover for beetles in temporary ponds. No field research is provided here. Rather, the wider literature is used to develop a framework and investigate how well the literature fills out the elements of the framework. This paper will take an unusual structure. First, lessons will be derived from other studies; second, a pathway will be proposed based on those lessons; third, the process of assessing the coverage of the literature will be described; and finally, the findings of the evidence map will be presented.

II. Lessons Gathered from Neighbouring Fields

Evidence from beyond the beetle literature is useful because few studies pair specialization with turnover in temporary waters. Six threads stand out.

2.1 Linked Habitats

Pecies of riparian spiders, which play an important role in the coupling of aquatic and terrestrial realms and are important predators, changed according to seasonality, mode of hunting and habitat specialization (Bollinger et al., 2023). That means specialization is not an isolated attribute and depends on other factors such as time and foraging strategies of consumers. Beetles, which have adults that leave and return to the pond, are also influenced by that linkage.

2.2 What Counts as Habitat

Reviewing natural and artificial freshwater habitats described features, impacts and management aspects of those places, and the implications for biodiversity conservation (Cantonati et al., 2020). The lesson here is that artificial water bodies are essential for conservation and bear unique pressures that need to be managed.

2.3 Timing as a Trigger

The explosive breeding of tropical anurans is stimulated by environmental triggers and affects community structure and acoustic structure (Ulloa et al., 2019). Beetle colonization can replace breeding as an environmental trigger.

2.4 The Time Window

Hammond and Kolasa suggested cumulative diversity, which accrues over time, and determined its drivers (Hammond & Kolasa, 2019). A single survey of a temporary pond would therefore underrepresent its diversity. The surveys must take place throughout the entire hydroperiod.

2.5 Management as a Filter

The impact of fish farming management on diversity of freshwater species was selective (Harabiš et al., 2023). This means that not all categories of organisms were affected equally. Management may function as a filter, with specialists as the obvious targets.

2.6 Benefits Beyond the Water

The construction of temporary waters resulted in an increased number of resources (food, nesting sites) for bees (Twerd et al., 2022). In other words, temporary waters may host non-aquatic organisms. This makes the preservation of such habitats more important.

These studies show three important gaps in the literature. The first one is related to the study of specialization in relation to turnover. Hydroperiod is considered a control variable rather than a design one. None of the twelve references mentions beetles in its title.

III. A Working Pathway from Drying to Turnover

Consists of four steps. Three are sequential steps while the fourth is a group of filters acting on those steps.

- **Stage 1, the Drying Filter.** There is a pulse of rainfall which creates the pond. The duration of the wet period, the hydroperiod, determines the first filter. Only organisms capable of developing or surviving the dry period will be able to persist. This functions according to the rule of functional response to temporality and the rules of rain-induced assembly.
- **Stage 2, Specialist–Generalist Sorting.** In the filtered pool, generalists which tolerate the conditions in the pool must be able to use pools along the hydroperiod spectrum. Specialists would be concentrated in places where specific needs are satisfied, and those places are likely to be long hydroperiod ponds.
- **Stage 3, Dispersal and Recolonization.** Once the ponds become rewetted, flight dispersal reconstructs assemblages from nearby pools and refuges. This brings together local pond communities to form a metacommunity.

Outcome, Community Turnover. The species replacement between ponds and between seasons within the pond is the outcome.

Modifiers. Fish predators have been found to change habitat preference, and this would be a different reaction for a specialist than a generalist. The source of the pond, either natural, artificial, or restored, will affect what is available for colonization.

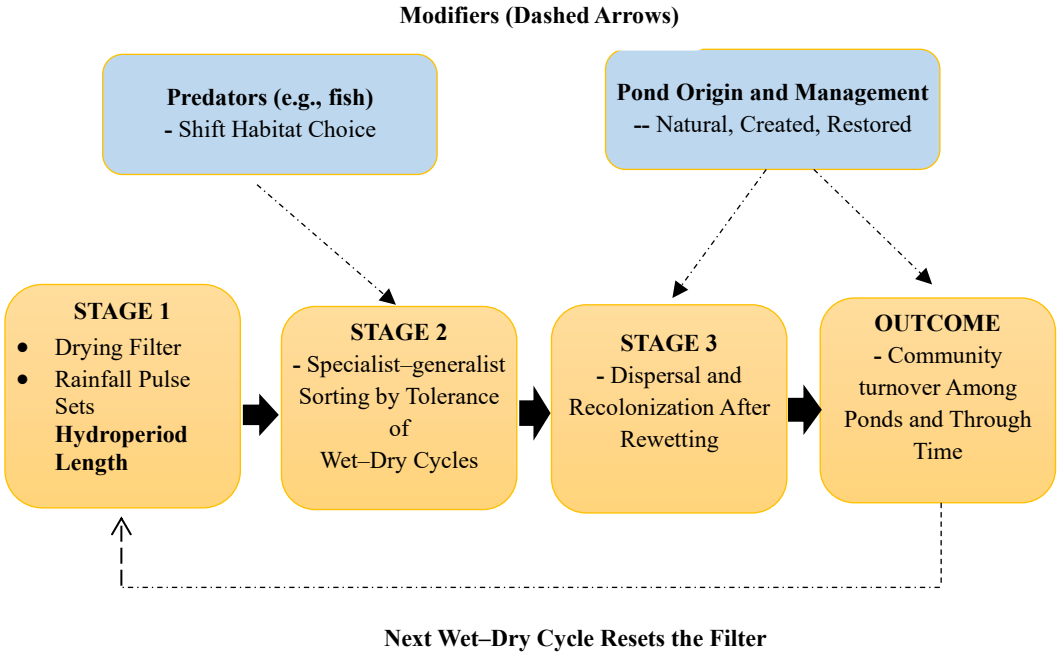


Figure 1:Conceptual Framework

Figure 1. Conceptual framework that relates drying, specialization-generalization sorting, dispersal, and turnover among temporary pool beetles, with predators and pond management as modifiers.

This model would result in four hypotheses that can be tested with field data:

- **H1.** Specialists will predominate in ponds with long and stable hydroperiods, whereas generalists will prevail in short ones.

- **H2.** There should be a higher turnover rate of ponds in ephemeral ponds and this process should be mainly influenced by replacement of generalists.
- **H3.** If there are fishes, specialists should avoid colonization and generalists should be less influenced by this factor.
- **H4.** Networks of created or restored ponds with different hydroperiods will host more species than uniform ponds.

IV. How Coverage of the Pathway Was Mapped

The comprehensiveness of coverage of the pathway in the existing literature was assessed through coding of the twelve articles used in this analysis. The corpus was provided as part of this analysis. It has not been gathered systematically from database searches, and no claim of comprehensive coverage of the literature is made.

Each article was read for its title and research question. Then it was coded, either yes or no, against five topics based on the pathway: hydroperiod and seasonality, community turnover, artificial or managed water bodies, habitat specialization, and predation. Each article was further sorted into one of four broader taxonomic classes: aquatic invertebrates, amphibians, terrestrial-linked consumers (spiders and bees), and multiclass or freshwater general.

Counts were performed for each topic by class, and the topics that occurred in any single article were recorded.

Clearly, this approach has limitations. The corpus was limited, a single coder performed the coding, and an article may be coded as missing a topic even when mentioning it casually. Thus, these counts provide an accurate description of the corpus, but not of the entire body of knowledge on the subject.

V. What the Evidence Map Shows

5.1 Thematic Coverage

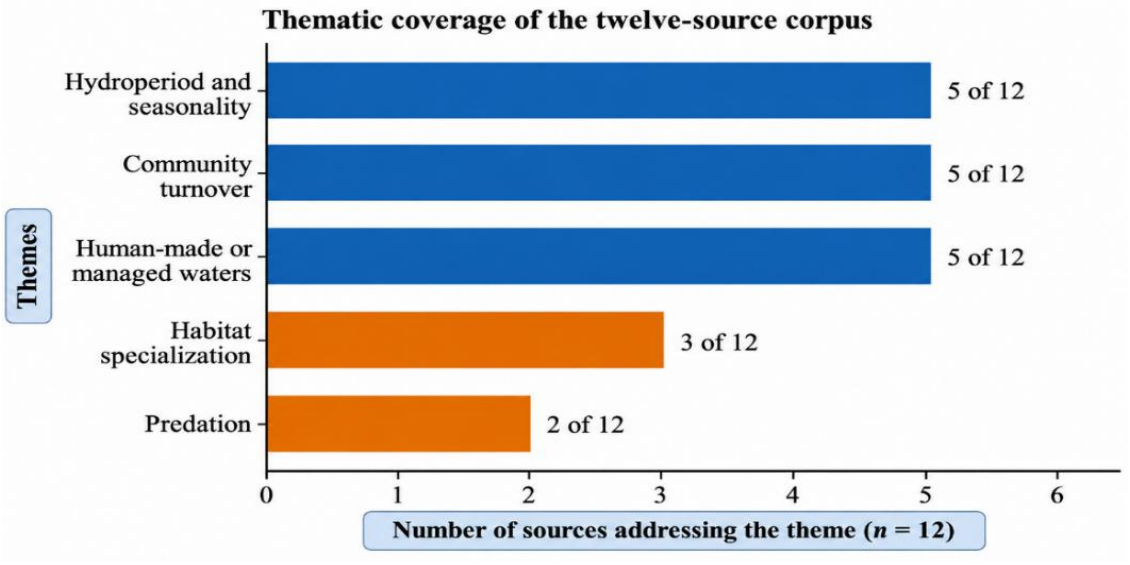


Figure 2: Number of Sources, Out of Twelve, Addressing Each Theme

Three topics discussed by five out of the twelve articles included water body duration, seasonality, and community turnover; human-made water bodies and predation in two sources each; and habitat specialization in three sources.

The thematic representation of twelve sources selected is provided in figure 2 with respect to five primary research topics. Topics that receive the highest number of references in sources include hydroperiod and seasonality, community turnover, and artificial or managed water, with five sources being dedicated to each of them. Habitat specialization is mentioned in three sources, which means it is a topic worth moderate research interest. Predation is the topic least mentioned in sources, with only two sources mentioning it. It can be concluded that existing research mostly revolves around seasonality, changes in ecological communities, and managed water.

5.2 Breadth within sources

Only five covered one theme, six covered two, and only one covered three themes, which comprised specialization, seasonality, and predation. On average, there were 1.7 themes per source. None of the sources covered more than three out of the five themes.

5.3 The missing link

Three sources that were coded for specialization and five for turnover are not similar; specialization and turnover were never covered simultaneously in any of the sources from this corpus. The phenomenon of predation was covered only in the two sources on semiaquatic and riparian predators.

5.4 Who is studied

Four sources were dedicated to aquatic invertebrates and multi-taxon studies; two sources were dedicated to amphibians, while terrestrial-linked consumers were covered by two sources. Different groups had different distributions of themes in figure 3 below. Studies of amphibians focused on turnover and hydroperiod and did not cover management. Studies of aquatic invertebrates covered hydroperiod, turnover, and managed waters, but did not include specialization and predation.

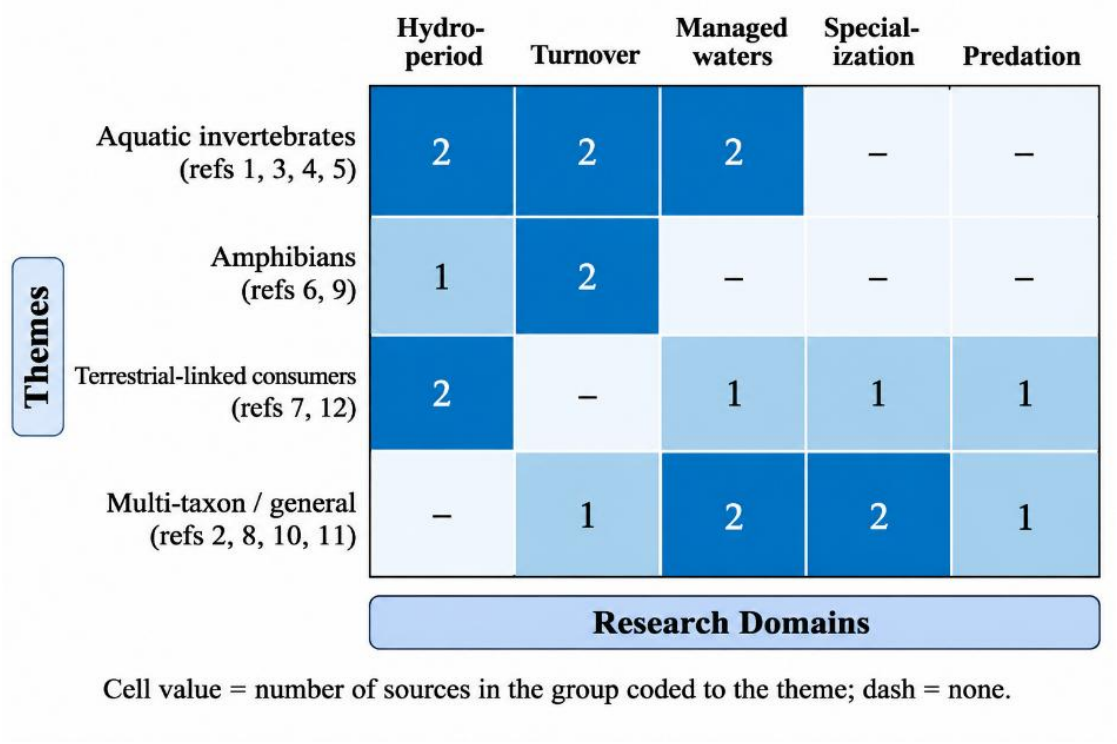


Figure 3: Number of Sources by Taxonomic Group and Theme

VI. Reading the Pattern

Clearly, the most apparent finding is the lack thereof. In fact, the body of literature under investigation sees specialization and turnover as distinct topics. However, for the mechanism shown in figure 1, there is one aspect common to both topics: the differences between specialists and generalists are what determines whether one gets replaced while the other remains. Investigations into species turnover in frogs and meiofauna are concerned with the driving factors behind species replacement and trait change. Investigations into specialization are concerned with differences in habitat selection and anti-predator behavior among the taxa. Combining these is the natural thing to do, and temporary ponds fit this perfectly.

The second outcome pertains to the heavy reliance of the corpus on hydroperiod and management. This is encouraging in that it suggests that the two factors that are most influential on the first and third steps of the pathway have been well represented in the literature. In addition, it suggests that the corpus has developed to a stage where management issues could be approached from the standpoint of hydroperiod, just as in the created waters literature. With only one hydroperiod in managed ponds, these ponds may provide only generalists and not specialists. This is a hypothesis, not an observation, and it is consistent with selective effects noted in managed freshwater.

The third outcome relates to time. The cumulative diversity and rain-induced assembly outcomes clearly highlight that the result obtained is highly dependent on when the sampling was done. Since some beetles disperse into ponds and others out of the ponds, a one-time survey of the pond is likely to give misleading results in either way.

There are also some limitations in the model as well. The model presumes the capacity of specialization assignment to species of beetles is consistent and there is a lack of definition of traits in the literature. In addition, it considers dispersal sufficient enough to reconstruct assemblages, but it is not true for isolated ponds. It considers predators and management as two distinct modifiers while in ponds on fish farms they coincide. Finally, since the map of the evidence base is based on twelve sources and one coder only, counts should be considered as descriptive.

VII. Conclusion

A number of practical suggestions can be drawn from the proposed model for managing ponds and conserving biodiversity. Managers of ponds must make sure to construct a diverse array of ponds with varied hydroperiods, meaning that not all ponds should be designed identically. This will allow different ponds to go through different stages of drying during different periods of time. Ecological monitoring must be carried out throughout the entire wet phase of ponds, starting from filling to total drying, which will allow for discovering species arriving at different points in time during the hydroperiod. Additionally, special attention should be paid to the dry period by recording potential beetle shelters in the form of soil, vegetation edges, and even terrestrial areas near the ponds. Ponds free of fish should be conserved since the presence of predatory fish would prevent specialist beetles from colonizing the pond. Also, artificial and restored ponds should be included in the conservation network, taking into account former management regimes and ecology.

Future studies would have to pursue three important directions to help fill the knowledge gaps highlighted above. Firstly, field studies will need to combine the study of beetle specialization categories with species turnover rates for various ponds and seasons to get a broader perspective of the community structure and dynamics. Secondly, hydroperiod would need to be treated as an important ecological and management factor by choosing and studying different ponds in relation to their various periods of drying and flooding. Thirdly, controlled experiments contrasting fish and no-fish ponds would be needed.

However, the fact that temporary ponds often attract less attention than other water bodies can be attributed to the high ecological importance of the former and the difficulty of recreating lost habitats. In this context, this investigation demonstrates that the understanding of the beetle communities in temporary

ponds depends on two interconnected ecological factors: the capability of certain beetles to occupy various pond habitats and the substitution of the species in case of multiple cycles of drying and filling of the ponds. While the current literature investigates these issues as independent lines of the research, the combination of these aspects can offer better knowledge. Thus, further beetle-oriented field studies that combine the above-mentioned factors can fill one of the significant gaps in science and provide stronger scientific data for conserving aquatic habitats.

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