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PRIMARY RESEARCH PAPER

Invertebrate beta diversity in permanent and temporary lentic water bodies: a meta-analytic assessment

Amanda Caroline Faustino de Queiroz · Maria Anton-Pardo · Luis Mauricio Bini · Adriano Sanches Melo

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Abstract Water bodies vary widely in terms of environmental stability, and most of this variation is due to water permanence. Permanent systems are expected to have a more stable community since the organisms will not be subjected to the severe disturbances caused by droughts. Temporary habitats are stressed by frequent dry phases, which reset the system and trigger succession processes that can drive changes in species composition. Previous studies have found higher beta diversity among permanent than among temporary water bodies, whereas others have found the opposite. We conducted a meta-analysis to compare the beta diversity of aquatic invertebrates in permanent and temporary water bodies and assess whether there is a predominant relationship between beta diversity and water permanence. Our results revealed that the beta diversity of invertebrates did not differ between permanent and temporary habitats. Primary studies showed both patterns: some of them presented higher beta diversity in permanent than in temporary water bodies, whereas others presented the opposite, resulting in a net effect of no difference. The lack of a clear pattern may result from the interaction with multiple factors, including hydrological specificities of the study areas, scales, and dispersal abilities

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A. C. Faustino de Queiroz (✉)
Programa de Pós-Graduação Em Ecologia e Conservação da Biodiversidade, Instituto de Biociências, Universidade Federal do Mato Grosso, Campus Cuiabá, Cuiabá, MT 78060-900, Brazil
e-mail: amandacarolfaustino@gmail.com

M. Anton-Pardo
GRECO, Institute of Aquatic Ecology, Faculty of Sciences, University of Girona, Campus 7 Montilivi, 17071 Girona, Spain

M. Anton-Pardo · L. M. Bini · A. S. Melo
Departamento de Ecologia, Universidade Federal de Goiás, Av. Esperança s/n, Campus Samambaia, Goiânia, GO 74690-900, Brazil

A. S. Melo
Departamento de Ecologia, Universidade Federal do Rio Grande do Sul, Av. Bento Gonçalves 9500, Porto Alegre, RS 91501-970, Brazil

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of the organisms investigated, as well as environmental and anthropogenic factors.

Keywords Community variation · Hydroperiod · Systematic review · Pond

Introduction

Environmentally stable aquatic ecosystems not limited by dispersal select species able to withstand biotic interactions, local conditions, and resource variability (Wellborn et al., 1996). Predation may reduce the sets of species that are able to persist in these ecosystems, whereas habitat complexity may buffer such effects by the provision of refuges (Diehl, 1992; Wellborn et al., 1996). Strong competitors may also increase local extinction rates, whereas high productivity may weaken such effects (Chase, 2010). Accordingly, environmentally stable habitats may, on the one hand, select specific sets of species through environmental filtering and biotic interactions, but on the other hand, they allow the coexistence of more species by providing more refuges as well as a higher diversity and quantity of resources. These opposing effects may increase (Sahuquillo & Miracle, 2019) or decrease local diversity (Chase & Knight, 2003), depending on the strength of each factor. Similarly, spatial variation in community composition (i.e., beta diversity) may be low if these deterministic factors in stable habitats select a restricted set of species from the regional species pool or high if coexistence mechanisms allow the occurrence of rare species through refuges or specific resources.

Environmentally dynamic systems may pose a barrier to the distribution of many species that are not able to cope with fluctuating conditions and resources (Leigh & Datry, 2017). For example, temporary aquatic systems are likely to filter species—from the regional pool—with a particular set of traits to withstand unfavorable environmental conditions and disturbances, including rapid life cycles and high colonization abilities (Gray, 1981; Wellborn et al., 1996). Accordingly, it may be expected that the same reduced set of species would colonize different sites, which would lead to a low beta diversity. On the other hand, these dynamic ecosystems, with constant resetting produced by harsh conditions or severe disturbances, may be subject to priority effects, i.e., the advantage that early colonists have independent of species identity (Vellend et al., 2014; Devercelli et al., 2016). Thus, priority effects would lead to a high beta diversity since they amplify the initial differences in community structure (De Meester et al., 2016).

Water bodies vary widely in terms of environmental stability, and an important part of this variation is related to water permanence or hydroperiod (i.e., the length of time that an area is saturated with water; Wellborn et al., 1996). Permanent systems are expected to have a more stable community since the organisms will not suffer from the severe disturbance caused by droughts. Those systems are usually large and deep, with high heterogeneity and many refuges, favoring the coexistence of different species and enhancing beta diversity (Baber et al., 2004). In those habitats, factors such as abiotic conditions as well as biotic interactions tend to be important in structuring local communities (Vinson & Hawkins, 1998). Predation is one of the most determinant interactions in ponds, particularly in permanent habitats where long-lived predators, such as fish, exert strong pressure on prey (Galatowitsch & Mcintosh, 2016). Predation can eventually cause local extinctions and generate variation among local communities. On the other hand, the hydrological stability of permanent habitats allows more time for such interactions to homogenize the communities via succession, resulting in a low beta diversity (Daniel et al., 2019).

Temporary water bodies undergo droughts that reset the system and trigger succession processes that drive changes in species composition and relative abundances (Galindo et al., 1994; Attayde & Bozelli, 1998; Widdicombe & Austen, 2001). The existence of a dry phase represents a challenge for species persistence, where it will require adaptations of the organisms to survive, in addition to capabilities to migrate or to transition to a terrestrial phase (Wellborn et al., 1996). These environmentally dynamic systems will constrain the presence of long-lived predators such as fish, reducing their effects on the community structure. Also, water intermittency may filter sensitive species, leading to a reduced set of taxa that can dominate the temporary sites and cause a low beta diversity in the metacommunity (Poff, 1997; Chase, 2007). On the other hand, these factors may result in high temporal variation in species composition due to different successional trajectories since the last drought; in this

case, snapshot sampling may reflect different successional stages and produce high spatial beta diversity if dry periods are not spatially synchronized (Anton-Pardo et al., 2019). Previous studies have reported contrasting results regarding the effect of water permanence on beta diversity. For instance, Chase (2007) and Lopes et al. (2014) found higher beta diversity among permanent ponds, whereas Schriever & Lytle (2016) and Daniel et al. (2019) observed that temporary sites exhibited higher beta diversity than perennial ones. In addition, Rosset et al. (2017) found no differences in beta diversity between permanent and temporary water bodies.

Aquatic invertebrates represent an interesting group for studies on the influence of water permanence on biotic communities (Soria et al., 2017; Anton-Pardo et al., 2019). Many invertebrates have adaptive traits, such as diapause or quiescence, to endure the drastic environmental conditions caused by droughts (Gyllström & Hansson, 2004 and references therein). For example, zooplankton groups can produce diapausing eggs or interrupt their development to cope with periods of harsh environmental conditions (Brendonck & DeMeester, 2003; Hansen, 2019). When the water levels increase and the environment becomes favorable again, they can restart their development. Similarly, active dispersers can migrate to more suitable habitats during drought periods and return when the water level rises (Williams, 1977).

The difference in invertebrate beta diversity between permanent and temporary habitats may depend on additional factors (Galatowitsch & Mcintosh, 2016). Dispersal ability and type may be decisive in environmentally dynamic systems since fast (active) colonizers may be widespread and decrease the community variation among sites (Chase, 2007). Also, major faunal differences may be associated with distinct biogeographic realms, and thus, responses observed in the North Hemisphere (and its Laurasian fauna) may differ from those derived from Gondwana and currently mostly present in the Southern Hemisphere (Upchurch, 2008; Toussaint et al., 2017).

Against the background of a changing climate, studies exploring the relationship between water permanence and changes in community composition are particularly important. Under increased climate variability, freshwater systems experience changing water regimes, either by intensifying rainfall or drought (Arnell, 1999; Kundzewicz et al., 2008; Junk, 2013; IPCC, 2021). Linking those changes with the variation in lentic communities can help to know how and why communities are structured in the present but also how they will respond to climate change (Boersma et al., 2016).

We conducted a global meta-analysis to compare the beta diversity of invertebrates between permanent and temporary lentic water bodies. While previous studies have produced mixed results, our meta-analysis assessed whether there is a relationship between beta diversity and water permanence. We also explored whether the effect sizes (i.e., standardized difference between permanent and temporary lentic waterbodies) are related to the dispersal type of aquatic organisms (active or passive), organism habitat type (benthic or planktonic), and region (Northern and Southern Hemispheres).

Methods

Selection of studies and data extraction

We based our search on a previous meta-analysis on alpha diversity, conducted by Anton-Pardo et al. (2019), and updated their data to include studies from 2017 until 2020. Thus, we conducted a systematic search to retrieve articles that compared the diversity metrics of aquatic invertebrates among permanent and among temporary lentic habitats. We used the Clarivate Web of Science database to update our dataset (August 23, 2020), including all databases and without restrictions of date, document type, or language. We used Boolean operators to combine search terms, which included permanent and temporary lentic habitats and synonyms such as "ephemer*" or hydroperiod*" for temporary and "standing water" or "lake" for permanent waters. We also combined these keywords with terms related to aquatic organisms, such as "zooplankton," "macroinvertebrate," as well as family, genus, or common names of frequent invertebrate taxa and terms related to diversity (e.g., "species richness") (Table S1).

Our search resulted in 2,531 records. Of these records, we excluded 1,932 articles because they did not meet our inclusion criteria (Fig. 1), namely: (i) the paper was out of the topic of the search (e.g., running waters or study of populations), (ii) all habitats were either permanent or temporary (i.e., could not be

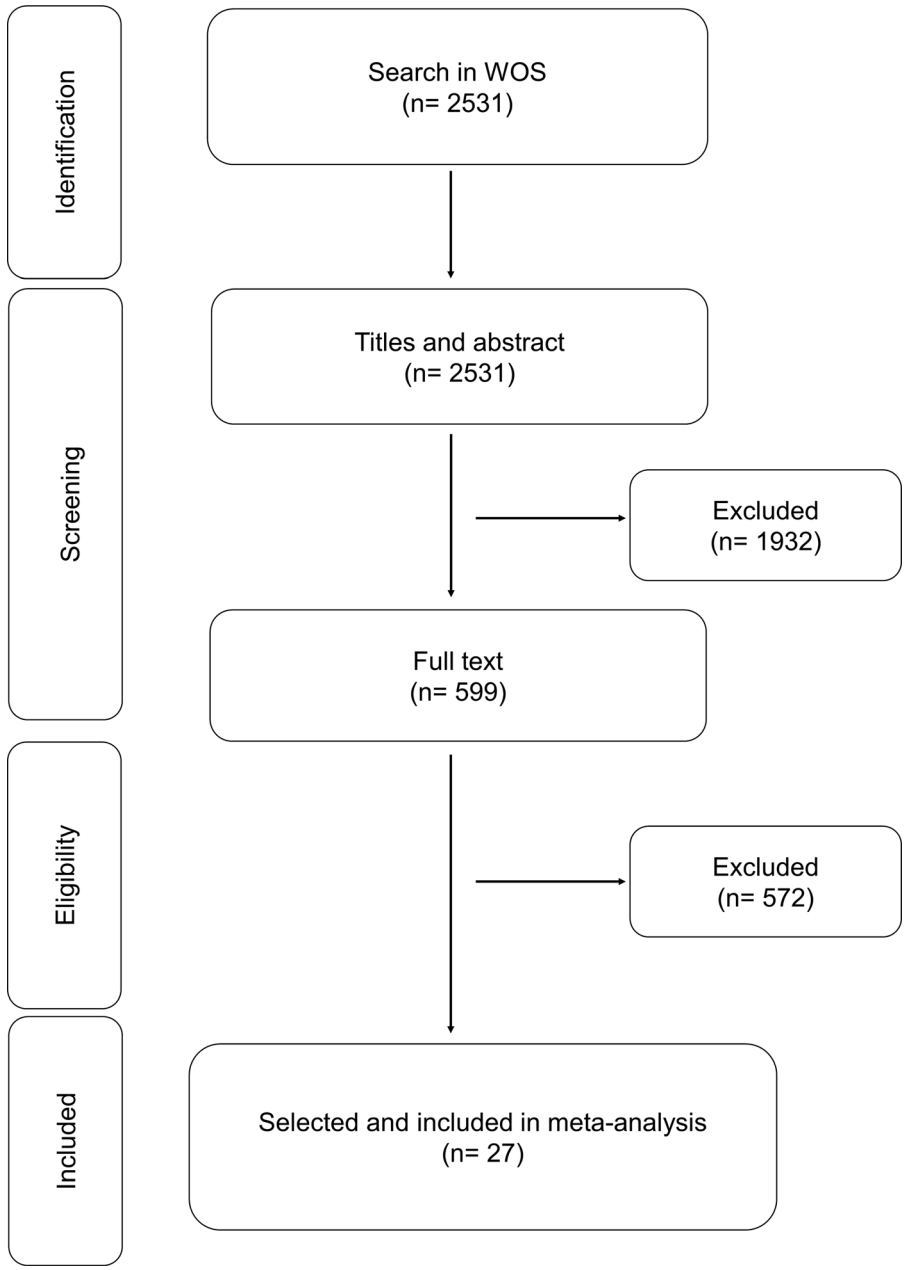

Fig. 1 Preferred Reporting Items for Systematic Reviews and Meta-Analysis (PRISMA; Moher et al., 2009) flow diagram summarizing study selection and exclusion in the meta-analysis of the 2531 articles obtained from the systematic search. One article included two independent datasets, and thus, 28 datasets were used for analysis

compared), (iii) the studied organisms were not invertebrates (e.g., terrestrial taxa, fish, phytoplankton), (iv) it was not a primary and observational study (i.e., reviews, experimental or laboratory studies); (v) species lists in each study site were not reported, or all taxa were identified with low taxonomic resolution (i.e., family or coarse levels); (vi) full text or data (i.e., species composition at each site) were not available, and the authors did not provide data upon request; and (vii) publications were not written in languages spoken by the authors of this study (i.e., only English, Portuguese, and Spanish publications were

considered). We re-screened each of the remaining 599 publications to select those relevant for the meta-analysis and that included explicit information regarding permanent and temporary habitats. We also included publications that contained information that allowed us to deduce that these habitats were investigated (e.g., authors named habitats as perennial or ephemeral). Temporary waters comprised all habitats having a drying phase (i.e., from semi-permanent to ephemeral habitats). After these steps, we retained a total of 27 articles for the meta-analysis. One article included two independent datasets (i.e., one from Finland and one from Poland; Iglikowska & Namiotko, 2012), and therefore, we used both of them in our analyses, resulting in 28 studies. For each article, we recorded the species composition per site and created a presence–absence data matrix.

Statistical analysis

We used the presence–absence matrix of each study to generate a Jaccard dissimilarity matrix. Then, using the *betadisper* function in the *vegan* package for R (Oksanen et al., 2017), we calculated the beta diversity of each type of habitat (permanent and temporary) as the average distance from each water body to its group centroid in an ordination space (Anderson et al., 2006). The larger the average distance, the higher the beta diversity. The standard deviation of the distances of the water bodies to their group centroid, permanent or temporary, was also recorded.

First, for each study, we calculated Hedges' g (see Borenstein et al., 2009) as the difference between beta diversity values in permanent and temporary water bodies. A positive value of g (i.e., positive effect size) indicates that beta diversity is higher among permanent than among temporary water bodies. Second, the weighted mean effect size (wES) was estimated with a random effects model (Borenstein et al., 2009). We also estimated two measures of heterogeneity between studies, T^2 and I^2. While T^2 is a measure of heterogeneity between studies, expressed in absolute values, I^2 is the proportion of heterogeneity between studies that is not due to sampling errors (Borenstein et al., 2009, 2017; Senior et al., 2016). Third, we ran a meta-regression to explore the effects of organism group (zooplankton versus benthos), type of dispersal (active versus passive), and geographic hemisphere (Northern versus Southern) on the effect sizes of the studies. Two studies were removed from this analysis because one included both types of dispersal and another included both zooplankton and benthos groups. Finally, we assessed the publication bias using the funnel plot and the "trim-and-fill method." The funnel plot consists of a scatterplot between the effect sizes against their standard error and allows visual inspections of whether there is publication bias (when the plot is asymmetrical) (Light & Pillemer, 1984). We used the "trim-and-fill" method to estimate the number of missing values that should be added to create a symmetrical funnel plot (Duval & Tweedie, 2000).

All analyses were performed in R 3.5.3 (R Core Team, 2019), using the package *vegan* (Oksanen et al., 2017) to calculate the dissimilarity matrices and beta diversity estimates and the package *metafor* (Viechtbauer, 2010) to estimate the effect size for each study, the wES, to test the moderators, and to analyze publication bias.

Results

The papers selected for our meta-analysis were distributed in all regions of the globe, but preponderantly in the Northern Hemisphere (19 out of 28 cases) (Fig. 2; Table 1). The articles were published during 1980–2019. The most studied groups were zooplankton (19 studies), aquatic insects (7), gastropods, and macrofauna (1 study each).

Beta diversity was higher in permanent than in temporary habitats in 12 studies (positive Hedges' g), whereas 16 out of the 28 studies showed negative Hedges' g, indicating that beta diversity was higher among temporary than among permanent habitats (Fig. 3). Of these 16 studies, 5 exhibited significant effect sizes. Overall, the wES was negative but not significant (wES $= -0.081$; 95% CI $= -0.299$, 0.136; $P = 0.463$), indicating that beta diversity did not differ between permanent and temporary water bodies. The total between-study variance (T^2) was 0.132, with 41.39% of this variance being possibly explained by other moderators (I^2).

Our meta-regression model indicated that studies focusing on zooplankton showed a significantly higher wES than those focusing on benthic organisms. Thus, the difference between permanent and temporary habitats was higher for zooplankton than for benthic organisms. Effect sizes (g) were unrelated to type of

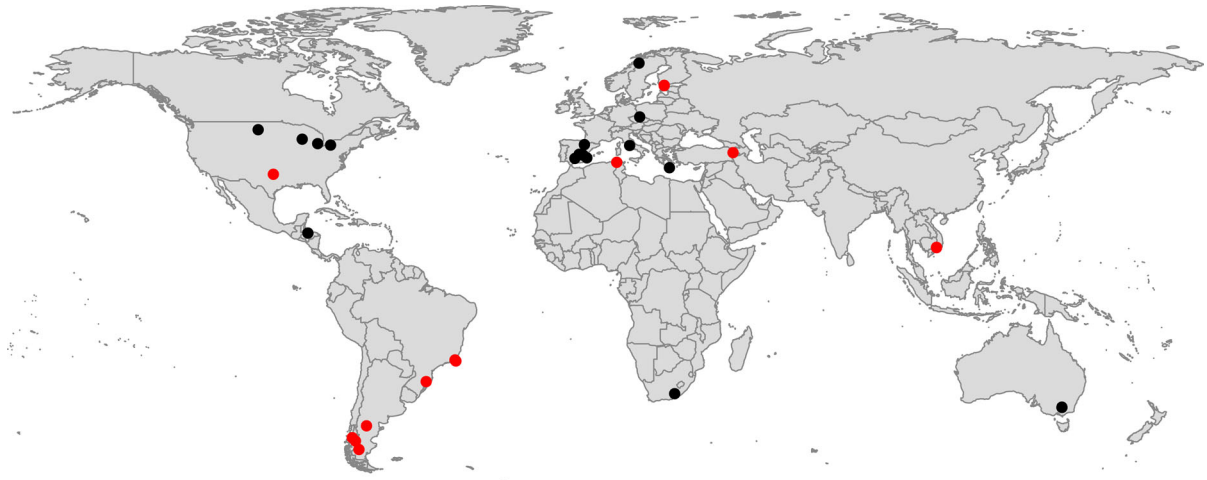

Fig. 2 Location of the studies included in the meta-analysis. Positive effect sizes (indicating higher beta diversity in permanent than in temporary waterbodies) are depicted in black and negative ones (higher beta diversity in temporary than in permanent waterbodies) in red

dispersal (active versus passive) or geographic hemisphere (Northern Hemisphere versus Southern Hemisphere; Table 2).

The trim-and-fill method indicated that no study would be necessary to produce a symmetrical funnel plot (Fig. 4).

Discussion

We did not find a significant difference between permanent and temporary habitats in terms of beta diversity. Although some studies have indicated a higher beta diversity in permanent compared to temporary water bodies, others indicate the opposite, resulting in no net difference between these habitats. However, we found that the difference between permanent and temporary habitats was dependent on the organism group, being positive for zooplankton and negative for benthic organisms.

Beta diversity among permanent habitats was higher than that among temporary counterparts in 12 studies, with one study showing a significant difference (Chase, 2007; Lopes et al., 2014). Other field studies found, however, that beta diversity was higher in temporary water bodies (e.g., Schriever & Lytle, 2016), paralleling the results of 16 studies that were included in our meta-analysis (five of them showed significant differences). Permanent habitats may allow a larger pool of species to colonize, and stochastic effects in colonization history, coupled with mild environmental filtering (in contrast to strong selection in temporary counterparts), can result in high beta diversity. In addition, permanent habitats usually are larger and deeper and include environmental heterogeneity, providing more refuges and, consequently, allowing the coexistence of more species (Baber et al., 2004). On the other hand, high beta diversity in temporary waters can result from the interruption in the succession process during periods of drought. It can generate high spatial community variation as a consequence of priority effects and different successional trajectories (Devercelli et al., 2016; Daniel et al., 2019). Since early colonists can have advantages, and the sequence in which organisms arrives can inhibit or facilitate the population dynamics of later arrivals, the variation in each community will be a result of each set of early colonists. Thus, depending on each initial assemblage, the final composition will be different (Vellend et al., 2014). Similarly, after drought resumes, different sets of species occupy the habitats but will be eventually homogenized by biotic interactions. However, the colonization process may not lead to similar communities if droughts are frequent or not synchronized.

The reduced effect of predation in temporary habitats seems to be one of the main factors shared by studies that contributed most significantly to Hedge's g and showed negative values (high beta diversity among temporary habitats; McCauley et al.,

Table 1 Characteristics of the 28 studies included in the meta-analyses

Study	Group taxa	Habitat	Type of dispersal	Geographic region
Schultz (2009)	Odonata	Benthic	Active	United States of America
Gilbert et al. (2015)	Branchiopoda and copepods	Zooplankton	Passive	Spain
Campbell et al. (2018)	Diptera	Benthic	Active	Australia
McCauley et al. (2008)	Odonata	Benthic	Active	United States of America
Turner et al. (2009)	Gastropods	Benthic	Passive	United States of America
Iglikowska and Namiotko (2012)—POL	Ostracods	Zooplankton	Passive	Poland
Elias-Gutierrez et al. (2006)	Cladocera	Zooplankton	Passive	Mexico, Belize and Guatemala
Marrone et al. (2019)	Crustaceans	Zooplankton	Passive	Greece
Mabidi et al. (2016)	Branchiopoda	Zooplankton	Passive	South Africa
Martinez-Garcia (2015)	Ostracods	Zooplankton	Passive	Northern Spain
Anton-Pardol et al. (2012)	Zooplankton	Zooplankton	Passive	Spain
Iglikowska and Namiotko (2012)—FIN	Ostracods	Zooplankton	Passive	Finland
Picazo et al. (2010)	Coleoptera	Benthic	Active	Spain
Carchini et al. (2007)	Odonata	Benthic	Active	Italy
Boronat et al. (2001)	Cladocera	Zooplankton	Passive	Spain
Schell et al. (2001)	Zooplankton	Zooplankton	Active–Passive	United States of America
Viayel et al. (2012)	Rotifera	Zooplankton	Passive	Iran
Annani et al. (2012)	Hemiptera	Benthic	Active	Algeria
Araujo et al. (2013)	Zooplankton	Zooplankton	Passive	Brazil
Verhoeven (1980)	Macrofauna	Benthic - Zooplankton	Passive	Netherlands, France and Mediterranean
Sinev et al. (2013)	Cladocera	Zooplankton	Passive	Vietnam
De los Rios (2008)	Zooplankton	Zooplankton	Passive	Chile
De los Rios et al. (2010)	Copepods and cladocera	Zooplankton	Passive	Chile
Lopes et al. (2014)	Zooplankton	Zooplankton	Passive	Brazil
Pires et al. (2017)	Odonata	Benthic	Active	Brazil
De los rios et al. (2018)	Zooplankton	Zooplankton	Passive	Chile
Drenner et al. (2009)	Zooplankton	Zooplankton	Passive	United States of America
Schwalb et al. (2002)	Ostracods	Zooplankton	Passive	Argentina

2008; Turner & Montgomery, 2009; Campbell et al., 2018). The persistence of organisms in permanent habitats could be constrained by predation, which selects similar sets of species across water bodies (Gilinsky, 1984; Diehl, 1992; Batzer et al., 2000). In temporary systems, high environmental variation usually reduces the abundance of predators or prevents colonization as they generally have longer life cycles (Turner & Montgomery, 2009; Campbell et al., 2018). Thus, high beta diversity among temporary systems seems to be a result of a trade-off between rapid growth to cope with droughts or extended development coupled to traits to avoid predation (Williams, 2006; McCauley et al., 2008).

Studies showing high and positive Hedge's g (high beta diversity among permanent habitats, e.g., Drenner, 2008; De los Rios et al., 2018) do not seem to share a particularly important factor. Instead, the high

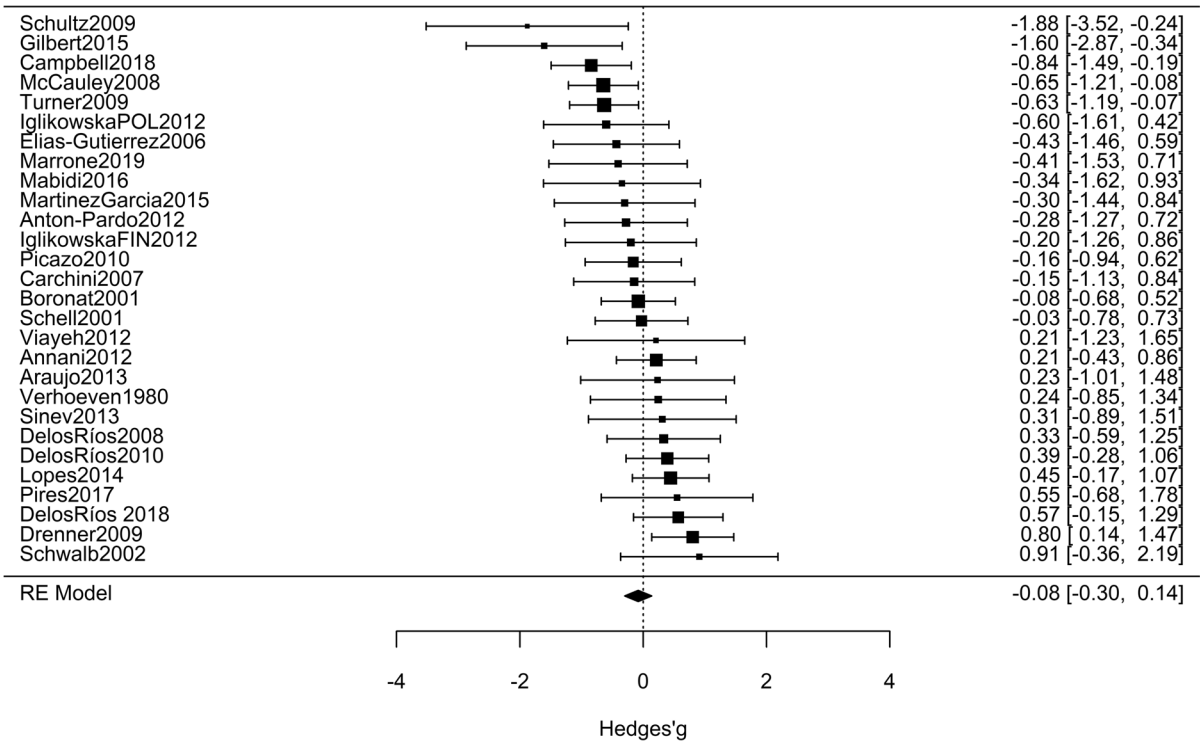

Fig. 3 Effect sizes (Hedges' *g*) and their corresponding confidence intervals (95%) for the 28 datasets included in the meta-analysis. Positive values indicate that permanent habitats showed higher beta diversity than temporary habitats. The sizes of the squares are proportional to the weight of the studies. The filled diamond at the bottom shows the weighted mean effect size (wES), with the edges of the diamond showing the corresponding confidence interval. The dashed line shows an effect size of zero

Table 2 Meta-regression results testing the relationships between moderators and effect sizes (Hedges' *g*)

Variable	Estimate	df	SE	CI_{95}low	CI95 up	*t*	*P*
Intercept	− 0.441	5.18	0.154	− 0.749	− 0.132	− **2.80**	0.005
Organism group (zooplankton)	0.639	10.79	0.315	0.020	1.258	**2.02**	0.043
Type of dispersal (passive)	− 0.192	5.18	0.325	− 0.830	0.445	− 0.59	0.554
Geographic location (Southern Hemisphere)	0.285	13.62	0.184	− 0.075	0.646	1.54	0.121

Reference levels for each variable are "benthos" for organism group, "active" for type of dispersal, and "Northern Hemisphere" for geographic location. Significant results ($P < 0.05$) are highlighted in bold

beta diversity among permanent water bodies likely reflects the individual characteristics of the studies. For example, a high beta diversity among permanent lakes may be associated with their trophic states, where those that can be classified as oligotrophic harbor high numbers of exclusive species (De los Rios et al., 2018). In this case, the high beta diversity among permanent habitats could be attributed to the niche specialization of the species. Also, permanent and deep habitats may show high beta diversity because fish may prey on specific sets of zooplankton species (Drenner, 2008).

Our results indicate that high beta diversity can be observed either among permanent or temporary habitats and that different mechanisms can explain each case. Thus, the difference in beta diversity between the two habitat types depends on other features of the environment or organisms. Despite the low number of

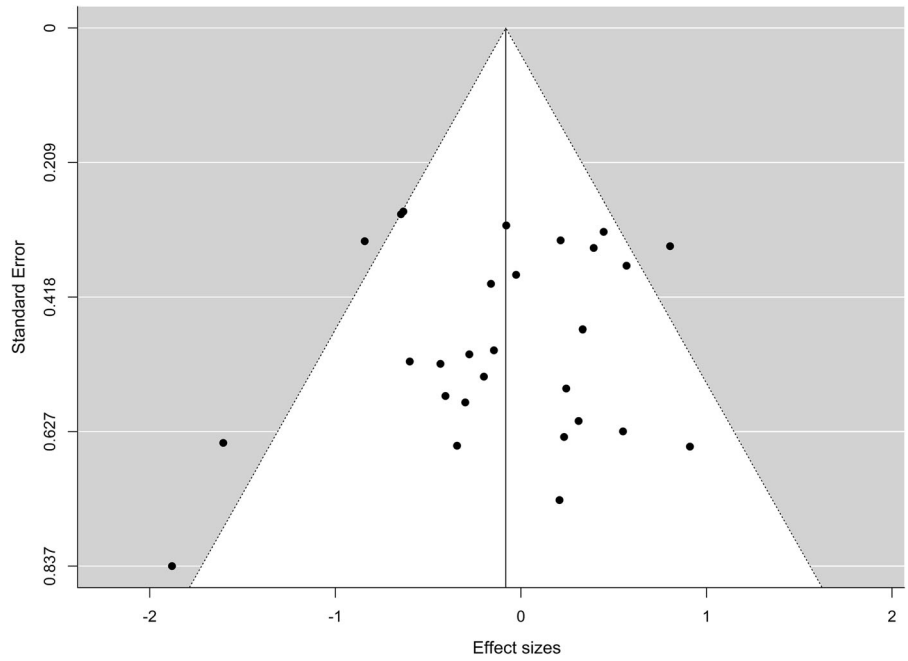

Fig. 4 Funnel plot of the studies evaluating the difference between permanent and temporary waterbodies in terms of beta diversity. Each study is represented by a filled circle

studies found in our literature search, we conducted an analysis to explore how effect size varies in relation to organism group (zooplankton versus benthonic organisms), dispersal (organisms with active versus passive dispersal), and geographic location (Northern Hemisphere versus Southern Hemisphere sites). We found that zooplankton beta diversity tended to be higher among permanent habitats than among temporary habitats, whereas the opposite occurred for benthonic organisms. The harsh conditions of temporary ponds may represent a strong environmental filter for the zooplankton community and select similar communities (e.g., only species with resting eggs or extremely high colonization capacity) (Hairston, 1996; Pinceel et al., 2018), whereas more species of benthic invertebrates would be able to tolerate droughts and/or colonize the site as soon as the water levels increase (e.g., adults of insects; Annani et al., 2012; Pires et al., 2017).

We did not find any differences between the effect sizes estimated for passive and active dispersers. Dispersal may overtake the importance of local environmental and spatial factors either for permanent or temporary water bodies (Heino et al., 2015). When the water level in temporary habitats recedes, active dispersers will move to more suitable habitats. Passive dispersers may die or remain in the habitat as dormant forms (Williams, 1977), causing composition variation among sites. Yet, dispersal mode was unimportant in the analyses. Also, the magnitude of the difference in beta diversity between permanent and temporary habitats was similar between Southern and Northern hemispheres. The lack of overall significance in our meta-analysis could have resulted from the fact that by integrating global studies, we overlooked patterns due to factors with opposing effects; yet these opposing effects were not dependent on the hemisphere in which the study was conducted.

The observation that a part of the studies showed significant effects (6 out of the 28 cases), but in opposite directions, indicates that they likely depend on other moderators. Our low sample size only enabled us to evaluate a few factors, and among them, only group of organisms resulted as important. Spatial extent is an additional factor that is usually associated with beta diversity. A larger spatial extent is associated with low connectivity and dispersal limitation, which may increase beta diversity (Heino et al., 2015). Unfortunately, we could not find such information in the primary studies (only 12 out of the 28 studies

included geographic coordinates of water bodies). Thus, we echo Gerstner et al.'s (2017) call for the need for detailed reporting on spatial scales (grain and extent) in primary studies.

Understanding how community variation occurs in both permanent and temporary habitats can help predict biodiversity distribution under climate change (Soria et al., 2017). Owing to the prediction that many permanent water bodies will become temporary (Larned et al., 2010; Datry et al., 2016; Reid et al., 2019), those changes can affect biodiversity. Previous meta-analyses comparing biodiversity in permanent and temporary waters concluded that the presence of a dry period decreases the number of species in temporary lotic (Soria et al., 2017) and lentic sites (Anton-Pardo et al., 2019). Because of the changes in the hydrological regimes, species in permanent water bodies will be lost assuming a low potential of evolutionary rescue (e.g., Bell, 2017). However, those effects can be much more severe for some groups, such as zooplankton as in our study, since the shift from permanent to temporary habitats could cause biotic homogenization. A reduction in beta diversity is also likely to reduce the capacity of the communities to be resilient and resistant to other disturbances (Olden, 2006).

Conclusion

Our results indicate that the difference in community variation among permanent and among temporary habitats was highly variable. Taken together, the beta diversity values associated with the two habitats were similar. The low number of studies limits a sound explanation of the factors underlying the difference between permanent and temporary habitats in terms of beta diversity. However, our exploratory analyses suggest that organism group may mediate the difference of beta diversity among permanent and among temporary water bodies, with zooplankton (in contrast to benthic invertebrates) presenting a higher beta diversity among permanent than among temporary habitats.

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Author contributions ACFQ and ASM conceived the ideas for this manuscript. MAP and ACFQ searched the literature and gathered the data. ACFQ conducted the analyses with the help of MAP and LMB. ACFQ wrote the first draft of the manuscript, and all authors contributed to it. All authors approved the final version of the manuscript.

Data availability The database used is available in the Supplementary Material section.

Declarations

Conflict of interest The authors declare that they have no conflict of interests.

Ethical approval Not applicable.

Consent to participate Not applicable.

Consent for publication All authors consent to the publication of this study.

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