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Review Paper

Dormancy and dispersal as mediators of zooplankton population and community dynamics along a hydrological disturbance gradient in inland temporary pools

Luc Brendonck · Tom Pinceel · Raquel Ortells

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Abstract At some stage in their life cycle, most zooplankton in temporary waters produce dormant eggs that assemble in a persistent egg bank to cope with unfavourable conditions. As part of a risk-spreading strategy, only a fraction of the egg bank hatches during a single inundation. Besides this dispersal in time, resistant dormant eggs also disperse in space via vectors including wind, water and animals. The structure and functioning of the dormant egg bank has important consequences for (meta) population and (meta) community structure and dynamics. Here, we merge empirical and theoretical data into a conceptual framework for the study of population and community responses in temporary ponds along a gradient in hydrological disturbance. Overall, we conclude that changes in hydrological disturbance may compromise both the abiotic (i.e. water quality) and biotic (i.e. population and community processes) integrity of temporary pools which is especially relevant in light of ongoing anthropogenic alterations in the hydrology of inland waters.

Keywords Egg banks · Diapause · Dispersal · Temporary pools · Zooplankton

Introduction

There are many different types of temporary aquatic systems that vary widely in their dimensions. Yet, all have in common is that they are transformed into a terrestrial habitat for a variable part of the year. Temporary aquatic systems, excluding rivers, are commonly referred to as temporary pools or temporary ponds, terms that will be used interchangeably in this text. Although they occur worldwide, they are

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L. Brendonck (✉) · T. Pinceel
Laboratory of Aquatic Ecology, Evolution and Conservation, KU Leuven, Ch. Deberiotstraat 32,
3000 Louvain, Belgium
e-mail: luc.brendonck@bio.kuleuven.be

L. Brendonck
Research Unit for Environmental Sciences and Management, North-West University, Potchefstroom Campus, Private Bag X6001, Potchefstroom 2520, South Africa

T. Pinceel
Centre for Environmental Management, University of the Free State, P.O. Box 339, Bloemfontein 9300, South Africa

R. Ortells
Institut Cavanilles de Biodiversitat i Biologia Evolutiva, Universitat de València, A. O. 22085, 46071 Valencia, Spain

most abundant in Mediterranean, arid and semi-arid regions with a distinct dry and wet season (Brendonck & Williams, 2000; Blondel & Aronson, 2005).

Temporary pools are generally characterised by a particular hydroperiod (duration of the aquatic phase, see Fig. 1; Table 1) which depends on the regional climate, pool dimensions, soil characteristics and extent of plant cover (Williams, 2006). Ephemeral pools are situated at one end of the permanence gradient. Such pools usually dry and get refilled several times during a wet season. Hydroperiods are consequently short and the timing, duration and frequency of inundations can be highly variable. Typical examples are temporary freshwater rock pools in (semi-)arid regions that occur in variable shapes and sizes on top of rocky outcrops (Brendonck et al., 2010, 2016). Intermittent pools generally also have several inundations during the wet season. However, their average hydroperiod is typically longer than that of ephemeral pools. Characteristic examples are Mediterranean peridunal ponds that largely depend on rainfall for filling and may be dry for several consecutive years (Olmo et al., 2012; Antón-Pardo et al., 2016). Further along the permanence gradient, seasonal pools are usually filled continuously during the wet season. Although the pattern of dry and wet phases is predictable, the exact start and length of the hydroperiod of seasonal pools vary both spatially, due to differences in pool and soil characteristics, and temporally, due to inter-annual climate variation. Hence, seasonal pools are more stable but still display both intra- and inter-annual variation in hydroperiod and inundation frequency. Typical examples are vernal pools that are filled during spring-snowmelt in

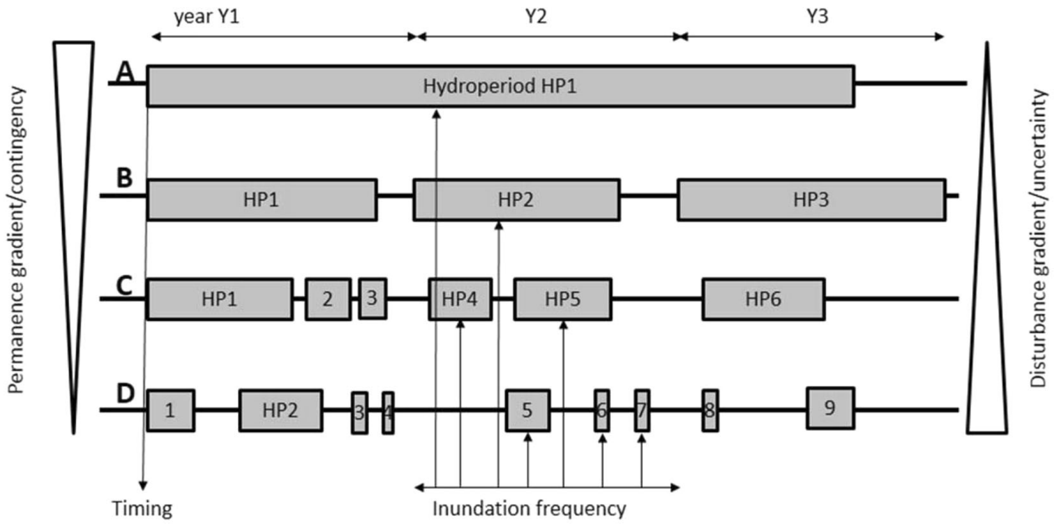


Fig. 1 Schematic presentation summarising the most frequently used characteristics of the hydroregime for four hypothetical types of temporary water bodies (sensu Williams, 2006): *A* near-permanent; *B* seasonal; *C* intermittent; *D* ephemeral. *Boxes* indicate the presence of water and *horizontal lines* represent dry periods

Table 1 Non-exhaustive glossary with commonly used terms to describe the phenology of temporary pools

Hydroperiod	Length of the wet phase of a pool
Successful inundation	Minimum hydroperiod needed to complete the aquatic phase of a species' life cycle
Inundation frequency	Number of times a pool floods during a time period (usually one season)
Permanence gradient	Hydroperiod gradient along which temporary pools are classified from ephemeral to near permanent
Hydrological disturbance	Frequency of successful inundations and average duration that pools contain water (or remain dry)
Timing	Moment of inundation
Predictability	Probability of a successful inundation when hatching conditions are optimal
Hydroregime	Hydroperiod and its variation, frequency and periodicity

temperate and boreal climates. Near-permanent pools are located at the far end of the gradient and can contain water for several subsequent years. They dry only due to exceptional weather conditions or human interactions like drainage. Although these are rather stable systems of long permanence, sudden droughts can still disturb and reset aquatic communities (Williams, 2006).

The hydroperiod and its variation, frequency and periodicity are merged in a complex variable termed hydroregime (Hulsmans et al., 2008). Due to its complexity, it is very difficult to describe patterns in abiotic and biotic temporary pool characteristics with respect to the pool hydroregime, and one should rather consider describing them in the light of more clear-cut hydrological characteristics such as the average duration and frequency of wet phases. As length and frequency of drought spells disturb the aquatic communities and can be perfectly interpreted in an ecological context, the term ‘hydroregime’ is often interchangeably used with ‘hydrological disturbance regime’ and will also be the preferred term in our review. Hydrological disturbance can be a dominant determinant of richness, composition and structure of the aquatic communities and genetic structure and life histories of the inhabiting populations (Wellborn et al., 1996; Brendonck et al., 1998; Boix et al., 2001; Eitam et al., 2004; De Roeck et al., 2010; Vanschoenwinkel et al., 2010a, b, 2013; Florencio et al., 2015; Antón-Pardo et al., 2016). Since pools that dry out and get refilled several times during a season usually occur in (semi-)arid climate regions with erratic rains while pools with a longer (and usually one) hydroperiod occur in more temperate regions with distinct seasonality (hence less disturbed seasonal pools), there will be a high correlation between hydrological disturbance and permanence (see Fig. 1; Table 1).

Temporary pools often house a remarkably high diversity of specialist species (Wiggins et al., 1980; King et al., 1996; Williams, 2006). Especially permanent residents such as zooplankton require some type of drought-resistant dormant life stage to bridge recurrent dry periods. These stages accumulate in the pool sediment in a so-called dormant propagule or egg bank from which the next generation can be recruited when suitable conditions are re-established. Depending on the hydroperiod, inhabitants can be faced with time-stress to mature and reproduce before their habitat dries and the active community is wiped out (Williams, 1996). Early pond drying can hence result in demographic catastrophes that represent a major threat in temporary pools and at the same time a dominant (life history) filter for colonists (Pyke, 2005; Vanschoenwinkel et al., 2013; Brendonck et al., 2015). Conversely, inundations are generally referred to as successful if the minimum hydroperiod to complete the aquatic phase of a life cycle is exceeded. The probability of experiencing a successful growing period depends on the organism’s life cycle and is therefore species specific.

While many studies have characterised the hydrology and fauna of some selected temporary pools from different areas, only some have compared pools along a disturbance gradient in one particular region (e.g. Serrano & Fahd, 2005; Jocqué et al., 2007; Waterkeyn et al., 2008; Boven & Brendonck, 2009; Vanschoenwinkel et al., 2009, 2013; Antón-Pardo & Armengol, 2010; Florencio et al., 2015; Brendonck et al., 2015; Antón-Pardo et al., 2016; Olmo et al., 2016). The approach of studying similar pool types along a hydrological gradient in one region reduces the impact of confounding factors and the unique effects of the disturbance regime can therefore be assessed more precisely. For example, rain-fed temporary rock pools usually occur in large numbers and different dimensions (depth and surface) on isolated outcrops in the landscape. Variation in dimensions results in variable levels of hydrological disturbance which, thanks to the relatively simple hydrology of the pools, can be reconstructed (Hulsmans et al., 2008; Vanschoenwinkel et al., 2009, 2013; Tuytens et al., 2014). Therefore, they have been used as a model system to assess specific effects of hydrology on population and community patterns (Tuytens et al., 2014; Brendonck et al., 2010, 2016).

In this review, we look for demographic and genetic signatures of dormancy and dispersal strategies at the population and community level across a gradient of hydrological disturbance in inland temporary pools. We first summarise a non-exhaustive set of definitions that are commonly used to describe the phenology of temporary waters, review different methods to quantify the hydroregime and composite hydrological variables and present the key faunal players of temporary pools. Second, we discuss dormant propagule bank dynamics with a special focus on hatching and dispersal strategies. We do not, however, attempt to present a general dormancy review (See Hairston, 1996; Cáceres, 1997a;

Brendonck et al., 1998; Brendonck & De Meester, 2003; Evans & Dennehy, 2005; Alekseev et al., 2007). Third, we investigate the importance of specific abiotic factors (e.g. water quality, space, predictability) and biotic processes (e.g. hatching, dispersal, competition, predation, founder effects, genetic erosion and inbreeding) in shaping population and community structure along the gradient of hydrological disturbance or its components and summarise and integrate all empirical evidence and theoretical assumptions in hypothetical and idealised diagrams.

Methodology and terminology

Whereas we have drawn-up a set of response patterns to several environmental characteristics along the hydrological disturbance gradient, it should be underlined that these patterns are not the result of a formal meta-analysis but of a non-systematic, qualitative review of the recent literature. Due to the complexity to describe ecological patterns with respect to hydroregime, we opted to use hydrological disturbance and disturbance regime or their composite variables, hydroperiod and frequency of inundations, throughout this review. Although we attempted to draw-up our conceptual framework for all zooplankters, cladocerans, large branchiopods and monogonont rotifers were the focal groups. The developed framework is intended to set out guidelines for future research, conservation and management in the light of global change. The main novelty of this review is that it is organised with hydrological disturbance as an integrating factor.

A non-exhaustive vocabulary with respect to the phenology of temporary pools is presented in Table 1. As for the definition of habitat predictability, we refer to the probability of a successful inundation when hatching conditions are optimal as this is the crucial factor to explain risk-spreading strategies. In a broader sense, predictability also refers to the variance in the timing of the wet phase.

Methods to characterise the hydroregime

Since hydroregime and disturbance regime are complex multidimensional entities, they cannot be estimated based on short-term observations. Only long-term monitoring over several decades offers reliable information that sufficiently incorporates temporal climatic variability including cyclic climate phenomena related to El Niño events (Brooks, 2004; Bauder, 2005). As it is not always possible to obtain such long-term measurements in situ, pool morphometrical variables are commonly used as proxies for hydrological disturbance including maximal depth, average depth and surface to depth ratio (Eitam et al., 2004; Jocqué et al., 2006; Antón-Pardo & Armengol, 2010). However, it is often hard to distinguish between direct effects of habitat size and hydrological disturbance through such an approach. Since long-term in situ monitoring of temporary pools over large spatial scales is logistically challenging, remote sensing imagery with optical (e.g. Landsat pictures available since last 30 years) or radar (e.g. Envisat) images have been introduced as a valid alternative. Such an approach can, however, be hampered by cloud cover and resolution constraints for small-sized pools. De Roeck et al. (2008) found optical (Landsat) images to be more accurate than Envisat and were able to compare number, size and distance between wetlands in the Cape region (South Africa) among the seasons but failed to detect small pools. In this respect, high spatial resolution images, such as IKONOS images for optical studies and RADARSAT-I and RADARSAT-II imagery for radar studies, could provide more detailed results (Wulder et al., 2004). However, these images are expensive and no long-term time series are available for a reliable reconstruction of the hydroregime. Landsat satellite recordings have recently become available, free of charge, allowing the scientific community to get access to a great deal of information without any cost (Asner, 2009). Several indexes have been developed to estimate the surface covered by water in Landsat scenes (Xu, 2006). Accurate interpretation of such images was facilitated through the development of radiometrical, geometrical and atmospherical corrections (Masek et al., 2006) that, for instance, allow to filter-out cloud, water and salt reflections (Zhu & Woodcock, 2012). Using time series from satellite images, the level of habitat predictability can be quantified based on two water presence components: constancy, a measurement of state permanence, and contingency, a measurement of the repeatability of the time pattern in successive years (Colwell, 1974). Based on Colwell's, and proposing new metrics, Franch-Gras et al. (submitted) used time series of Landsat-5 and Landsat-7 images to quantify habitat predictability from a system including 20 ponds in central Spain.

A reliable method to accurately reconstruct or predict the hydroregime of individual pools is by making use of hydrological models. A family of simple models has been developed to reconstruct the disturbance regime of rock pools based on long-term climate data and pool morphometry (Hulsmans et al., 2008; Altermatt et al., 2009; Vanschoenwinkel et al., 2009; Tuytens et al., 2014). Calibration and validation of these models, however, require time series of water level measurements. New model extensions not only assess water levels and the length of aquatic phases, they also allow estimations of the number of times a pool overflows or receives overflow water from neighbouring pools and the volume of water that is transported. In addition, model extensions generate proxies for certain water characteristics, such as conductivity, that may be crucial determinants of hatching and survival of zooplankton (Tuytens et al., 2014). Long-term hydrological variation reconstructed by such a model was a superior predictor of community patterns in South African rock pools than short-term hydroperiod observations (55 vs. 32%) (Vanschoenwinkel et al., 2009). The development and application of hydrological models is rather simple for rock pools, with rainfall and evapotranspiration as the major inputs and outputs, respectively. However, the construction of similar models for larger wetlands with muddy substrate and partial dependence on groundwater interactions is far more complicated (Pyke, 2005).

The key players and their typical life cycle

Permanent inhabitants of inland temporary pools typically include rotifers, water fleas, large branchiopods, copepods and ostracods. Other permanent inhabitants of temporary waters, including flatworms, gastrotrichs, nematodes and tardigrades, were not specifically included in this review. All permanent inhabitants of temporary pools produce some kind of dormant resistant egg or a more advanced developmental stage to bridge dry phases of their habitat (Williams, 2006). They not only rely on dormant propagules for recolonisation of their habitat upon filling, but also for dispersal to and colonisation of other pools (Brendonck & De Meester, 2003; Incagnone et al., 2014; Walsch et al., 2014, 2016). Although all permanent inhabitants produce dormant propagules, they occur at different stages in their life cycle, depending on the taxon (Cáceres, 1997a; Gyllström & Hansson, 2004).

Large branchiopod crustaceans are generally obligatory sexual and oviparous, exclusively producing dormant eggs (Brendonck et al., 2008). Ostracods include sexual and parthenogenetic species, with most families (except Darwinulidae) comprising species that produce dormant eggs (Cohen & Morin, 1990; Horne & Martens, 1998). In contrast to monogonont rotifers that undergo a true internally controlled embryonal diapause stage (resting egg), the bdelloids progress into a quiescent anhydrobiotic xerosome (Ricci & Caprioli, 2005). Except for some strictly asexual lines, most cladocerans and monogonont rotifers display cyclical parthenogenesis, and usually first produce asexual (clonal) offspring of directly developing eggs before switching to the production of males and sexual dormant eggs (Ricci, 2001; De Meester et al., 2004; Schröder, 2005; Decaestecker et al., 2009; Serra & Snell, 2009). The switch to sexual reproduction is induced by changes in the environment that signal less favourable food conditions, temperature, photoperiod, increased population density or predation risk (Carmona et al., 1993; Dumont & Negrea, 2002; Stelzer & Snell, 2003; Decaestecker et al., 2009). However, obligatory sexual taxa and amphoteric females have also been reported in rotifers (Gilbert & Schreiber, 1995, 1998; Schröder et al., 2007; Walsh et al., 2016) and cladocerans (Cáceres & Tessier, 2004; Decaestecker et al., 2009). The production of dormant eggs increases in importance for monogonont rotifers with decreasing hydroperiods as was experimentally shown in *Brachionus* (Pallas, 1766) by Smith and Snell (2012) and in *Hexarthra* (Schmarda, 1854) from rock pools by Schröder et al. (2007). Early mixis likely provides a long-term adaptive strategy for population persistence in ephemeral habitats that may dry up within a few days or weeks after filling. Exceptionally, the capacity of producing dormant eggs is uncoupled from sexual reproduction, and asexuality has appeared in some taxa by contagion, hybridisation or spontaneous mutation (Decaestecker et al., 2009; Serra & Snell, 2009). This obligate parthenogenesis probably evolved as an adaptation to very ephemeral habitats, in order to produce diapausing eggs quickly without the need of a male (Decaestecker et al., 2009).

Calanoid copepods share aspects of both the large branchiopod and rotifer/cladoceran life cycles; they reproduce sexually and switch from the production of immediately developing subitaneous eggs to dormant eggs in response to cues that signal unfavourable conditions, such as predation or drought (de Stasio, 1989; Hairston et al., 2000). Dormant stages are larval (copepodite stages) in the cyclopoid and adult in some harpacticoid copepods. Also, bdelloid rotifers are capable to enter dormancy in the adult state (Ricci, 2001; Ricci & Caprioli, 2005).

Awakening

After deposition, dormant eggs can remain floating but most sink to the bottom of the pool and are added to the dormant egg bank in the sediment (Brendonck & De Meester, 2003; Pietrzak & Slusarczyk, 2006; Cáceres et al., 2007). Zooplankton eggs can maintain dormancy for a variable period in a state of diapause which is an internally controlled phase during which they are unresponsive to their environment (Brendonck, 1996; Hairston & Kearns, 2002). While in diapause, the encapsulated embryos are most resistant and can overcome extended periods of drought or other harsh condition (De Stasio, 1989; Brendonck, 1996; Hairston, 1996; Kotani et al., 2001; García-Roger et al., 2006a). When a habitat is refilled, typically only part of the eggs hatches and contributes to the active community (Cáceres & Hairston, 1998; Gyllström & Hansson, 2004). Dormant eggs that are responsive are usually termed quiescent eggs. They require specific stimuli including light, a suitable conductivity level and temperature to hatch (Minkov et al., 1983; Pourriot & Snell, 1983; May, 1987; Brendonck, 1996; Pinceel et al., 2013a). Unhatched eggs can remain viable in the persistent egg bank and function as a buffer in case pools dry before hatchlings get mature or are able to produce dormant eggs (Hairston, 2000). Zooplankton egg banks were shown to buffer against population extinction during as many as 16 consecutive abortive hatching events (Brendonck et al., 1998). Extended dormancy is, however, not without risk. Often, viable eggs are buried in sediments that are stratified, and the likelihood of receiving hatching stimuli drastically decreases (Brendonck, 1996; Cáceres & Hairston, 1998; Cáceres & Tessier, 2003; Pinceel et al., 2013a). In addition, García-Roger et al. (2006c) reported a decreasing hatching fraction with sediment depth due to predation, senescence, disease, parasitism and increasing deterioration.

Habitat predictability and hatching strategies

Delayed hatching has often been observed in dormant zooplankton eggs (Brendonck & De Meester, 2003; Evans & Dennehy, 2005; García-Roger et al., 2014; Martínez-Ruiz & García-Roger, 2015) and most likely results from a combination of two mechanisms: phenotypic plasticity and bet hedging (cf. annual plant seeds; see Simons, 2014). The capacity of a single genotype to produce multiple hatching phenotypes can represent an efficient strategy to deal with variation in environmental quality including a variable risk of early drying (Spencer & Blaustein, 2001; Brendonck & De Meester, 2003; Evans & Dennehy, 2005; Vanoverbeke & De Meester, 2009; García-Roger et al., 2016). If future growing conditions are predictably announced by cues, conditional hatching through phenotypic plasticity may evolve (Pigliucci, 2001; Spencer & Blaustein, 2001). That way, eggs could refrain from hatching in the presence of cues that signal a high probability of early drying, whereas they leave dormancy if conditions announce a long inundation. Yet, if the conditions at the moment of filling are unreliable predictors of the length of the inundation (i.e. the habitat is not predictable), partial hatching may evolve as a bet-hedging strategy (Cohen, 1966; Seger & Brockmann, 1987; Philippi & Seger, 1989; Ellner et al., 1998). Through bet hedging, parents can buffer against unpredictable reproductive catastrophes on the long term, by ensuring that only part of their offspring hatches at the onset of any inundation (Evans & Dennehy, 2005). Although such a strategy may entail a potential loss of immediate fitness, it is beneficial for long-term fitness (Serra & King, 1999; Serra et al., 2004; Campillo et al., 2011). Theoretical bet-hedging models predict that as the reliability of hatching cues that signal early drying decreases, the potential for adaptive plasticity decreases and the investment in bet hedging should increase (Cohen, 1966; Spencer et al., 2001; Maffei et al., 2005; Schröder, 2005; García-Roger et al., 2006b; Venable, 2007; García-Roger et al., 2014). Therefore, hatching fractions should be negatively related to habitat predictability (Table 2b), although for this, it has been difficult to provide empirical evidence (see Brendonck & Riddoch, 2001; Vanschoenwinkel et al., 2010a; Simons, 2011; García-Roger et al., 2016). It is worth noting that habitat predictability does not always imply drying of the pond, because an organism's growing season is not necessarily coincident with the length of the hydroperiod, it can also be related to the presence of competitors or predators (García-Roger et al., 2016).

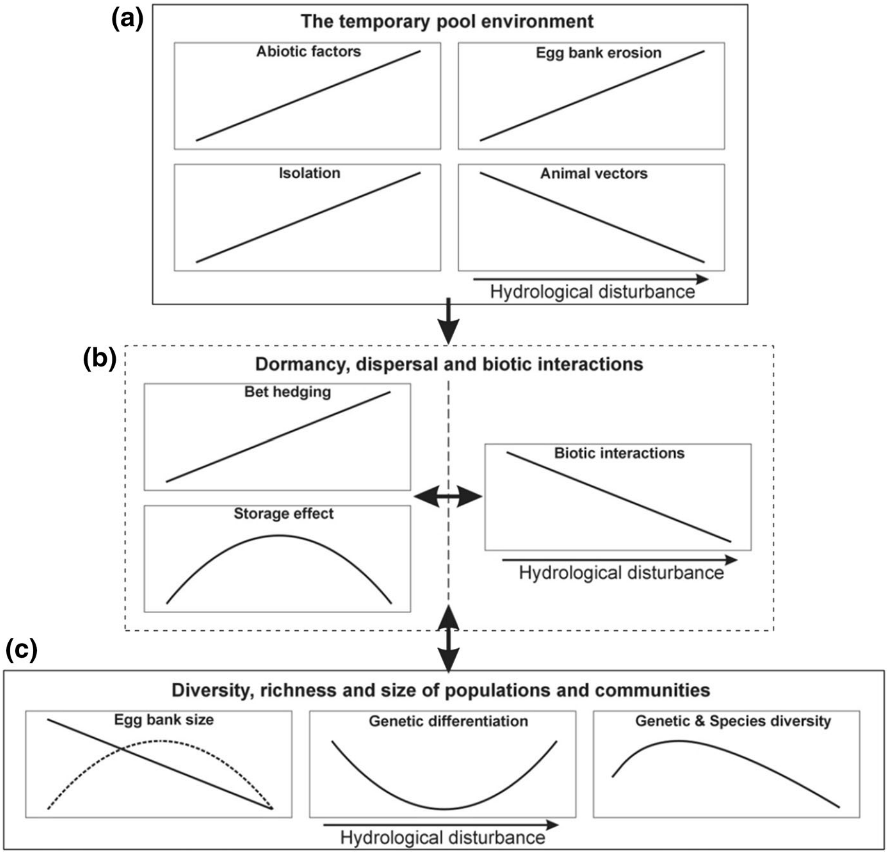
Strong empirical studies disentangling the relative contribution of phenotypic plasticity and bet hedging to hatching patterns in dormant zooplankton eggs along gradients in habitat predictability are deficient (Simons, 2011). Most information can be drawn from a number of field and laboratory hatching studies on fairy shrimp populations from temporary rock pools. *Branchipodopsis wolfi* (Daday, 1910) fairy shrimp populations from temporary rock pools in South Africa and Botswana inhibit hatching in response to high conductivity (concentration of salts) of the water (>125 µs/cm) (Brendonck et al., 1998). This could represent an adaptive strategy to avoid hatching when the likelihood of early drying is high, since elevated conductivity levels at the onset of an inundation signal a high probability of early drying (Vanschoenwinkel et al., 2010a). However, even if conductivity levels at the onset of the inundation are low, some inundations will still fall short without additional rains (Tuytens et al., 2014). Therefore, the quality of an inundation will be uncertain and selection should favour bet-hedging genotypes (Table 2b). Consistent with this notion, Vanschoenwinkel et al. (2010a) demonstrated that, even under optimal conductivity conditions, *B. wolfi* populations display partial hatching. In addition, Brendonck & Riddoch (2001) showed that under optimal conditions hatching fractions of *B. wolfi* populations from rock pools in Botswana roughly corresponded with the probability of a successful growing cycle as reconstructed from long-term rainfall patterns and averaged over all populations. In other temporary pond systems, an anecdotal study showed that intraspecific variation in hatching fraction between two fairy shrimp species, *Streptocephalus woottoni* Eng et al., 1990 and *Branchinecta sandiegonensis* Fugate, 1990, could be explained by differences in habitat predictability and selection for bet hedging between the pools where both species occur (Eng et al., 1990; Simovich & Hathaway, 1997; Philippi et al., 2001). In addition, Zarattini (2004) demonstrated that a population of the fairy shrimp *Chirocephalus diaphanus* Prévost, 1803 from a semi-permanent pond hatched more frequently than a population from a much more ephemeral pond with erratic hydroperiods, which implies a different investment in bet hedging.

In rotifers, variable hatching responses have been described (Pourriot & Snell, 1983), even under predictably good conditions, both at the level of individuals and of populations (García-Roger et al., 2016). At the individual level, Schröder (2005) and Martínez-Ruiz and García-Roger (2015) experimentally demonstrated within-clone variability in hatching response and proposed laying order (clutch number) as the proximate factor explaining the observed variation, with eggs that were produced first exhibiting longer diapause. At a regional scale, among-population differentiation in the hatching fraction has been reported (García-Roger et al., 2006b). Rotifer temporary populations from 13 pools in Eastern Spain showed a significant positive correlation between hatching fraction and species richness or pool depth (García-Roger et al., 2014), which are assumed to be good proxies for habitat predictability (Slobodkin & Sanders, 1969). In Iberian temporary ponds with variable hydrology, Walsh et al. (2014) observed hatching rates of branchionid rotifers that were lower in more permanent ponds, which is in contrast to theoretical predictions on optimal hatching rates and observations in branchiopods. As rotifers have a short life cycle, ponds that are ephemeral for e.g. large branchiopods may be of a much higher permanence level in rotifers, whereby hatching percentages are probably more determined by other (biotic disturbance) factors such as competition and predation that may also drive unpredictable demographic catastrophes.

Hydrological disturbance and dispersal

Besides serving to bridge unfavourable periods through time via dormancy, dormant eggs are generally also the dominant zooplankton dispersal propagules. They rely on vectors including water, animals and wind for their pick-up and transport (Bilton et al., 2001; Incagnone et al., 2014). Dispersal as an ecological process may be an important mediator of

Table 2 Text box



Generalised expected patterns of the importance of several environmental characteristics in shaping local populations and communities of permanent inhabitants of temporary pools along an increasing gradient of hydrological disturbance, from near-permanent to ephemeral temporary waters. Hydrological disturbance is here defined to be strongly determined by the duration and frequency of inundations. Along the same gradient, pools also usually (but not always) vary from a more to a less predictable nature. Diagrams project the importance of processes along the disturbance gradient at the level of the temporary pool habitat (a), and of the permanently inhabiting populations and communities (b) and their expected effect on structure and function of dormant and active populations and communities (c). For each of the diagrams, the underlying empirical findings or the theory for making idealised projections are explained in the text. Future studies will further fine-tune and falsify these often still hypothetical projections by means of more field work and meta-analyses so that also confidence limits can be generated for each diagram. As shown in several field studies, abiotic variables are generally more important in highly disturbed ephemeral systems (a), while biotic interactions become the dominant filter for population and community processes in more stable temporary pools (b). Along the same gradient, and especially frequently studied in rock pool species, hatching fractions from the mixed dormant egg bank decrease with increasing disturbance as risk-spreading processes like bet hedging become more important in unstable and less predictable pools (b). As predicted from theory and increasingly confirmed in controlled experiments, activation of the dormant propagules is determined by internal (diapause) factors in highly disturbed systems, while the importance of plasticity increases in more stable and predictable water bodies. Dispersal as a spatial risk-spreading strategy is especially important for population and community processes in the more ephemeral highly disturbed systems, because they frequently fall dry and are exposed to wind erosion as illustrated especially with rock pool systems (a). There is an interaction between disturbance and isolation of pools with more impact of dispersal in ephemeral systems that are geographically isolated (a). This is especially important for clustered pool systems like rock pools on inselbergs. As frequently shown with field studies on different temporary pool types, with increasing hydroperiods, more time is available for (re-) colonisation of the habitat by *in situ* hatchers and immigrants, resulting in an expected increase in genotype and species richness with time (c). However, with time, there is also an increase in predation pressure and clonal erosion, resulting in a drop in diversity in more permanent systems (c). In addition, intermediate disturbance is expected to have a positive impact on species

Table 2 continued

and genetic diversity, mediated by the storage effect (b). Here the nature of the disturbance should be clearly defined with respect the specific life cycle of the species considered. Due to a higher turn-over in more disturbed pools, chance processes will be more important than in pools with longer hydroperiods, resulting in lower genetic diversity due to genetic drift and inbreeding and increased genetic differentiation because of persistent founder effects, as confirmed also in limited field studies (c). In semi-permanent systems, in turn, we also expect lower genetic diversity within- and genetic differentiation among populations due to local adaptation and loss of genotypes in later inundation stages (c). Although there is a strong interaction with plant cover, we hypothesise that egg bank sizes in obligatory oviparous and sexual large branchiopod populations would be largest at intermediate levels of disturbance (c - dashed line). In ephemeral pools, inundations are frequently too short for successful egg production, while in later stages of long lasting pools, large branchiopods have ended their life cycle or are predated upon by immigrant insects. As revealed by many field studies, inferior competitors like the cladocerans, rotifers and copepods are taking over in later stages of the aquatic phase when large branchiopods are gone. We therefore expect larger egg bank sizes for these groups in longer lasting pools (c—full line)

population and community dynamics in response to hydrological disturbance. For instance, it may, via mass effects, affect the recovery rate of temporary pool communities after a series of unsuccessful growing seasons due to early drying (Ng et al., 2009; Vanschoenwinkel et al., 2013). In case of spatio-temporal variation in habitat quality, the production of offspring with variable dispersal propensities may serve to buffer against local demographic catastrophes in a metapopulation context (Siewert & Tielbörger, 2010). Therefore, it could serve as a spatial alternative to bet hedging via partial hatching where offspring is spread over multiple locations to buffer against occasional local catastrophes. Given these assumptions, a trade-off has been predicted between dispersal propensity and investment in dormancy (Cohen & Levin, 1987; Snyder, 2006). Therefore, propagules with high dispersal capacity should also hatch more readily in order to quickly colonise new habitats. However, solid empirical support for this potential evolutionary trade-off in zooplankton is lacking (Pinceel et al., 2013b). Whereas Pinceel et al. (2013b) found that dispersal prone (i.e. floating) eggs of the fairy shrimp *B. wolfi* were characterised by higher hatching probabilities, the dispersal propensity of eggs changed between inundations. This variation in hatching could be due to small differences in hatching cues that are experienced by floating and sinking eggs and should therefore not be interpreted as support for an evolutionary trade-off between dispersal and dormancy.

Direct field interceptions of propagules show that wind, water connections and animal vectors are of variable importance for transport, depending on the hydrological disturbance of the pool (Vanschoenwinkel et al., 2008a). Wind as a vector is expected to be far less important for more permanently flooded systems, where water connections and animal vectors are more dominant (Table 2a). However, for organisms with a drought-resistant dormant stage, drying might promote wind dispersal (Vanschoenwinkel et al., 2008a; Altermatt et al., 2009). Vanoverbeke et al. (2007, 2008a) observed that the number of dispersing propagules and taxon richness collected by means of wind socks planted along a South African rock pool cluster increased with the total number and surface of pools that were dry at the moment of observations. Wind speed was of secondary importance. It was therefore concluded that pools that dry out more frequently may serve more as sources of propagules while more permanently inundated ones serve more often as sinks (also reflected in Table 2a). Furthermore, Altermatt and Ebert (2010) revealed that small and ephemeral pools contributed to more than 90% of all dormant stages (ephippia) exposed during desiccation events in an entire metapopulation. They indicated this prominent role of small water bodies as drivers of metapopulation dynamics as an “inverse mainland-island type metapopulation”.

Little is known on variation in wind dispersal propensity among species and propagule types and whether there may be species-specific differences in the impact of drought spells on the egg banks exposed to wind action. By comparing the size and type of propagules travelling near the surface of an inselberg rock with those travelling at about 1.5 m height, Vanschoenwinkel et al. (2009) revealed that larger propagules (such as adult ostracods and oribatid mites) mainly tumble along the substrate, while smaller propagules (e.g. small resting eggs and cryptobiotic life stages of copepods) were collected in wind socks above the rock surface. Although they were not collected in this study, we also expect small rotifer eggs (monogononts) and cryptobiotic adults (bdelloids) to be apt for wind dispersal. That is also suggested by the fast (less than 7 weeks) colonisation by rotifers (10 species) of experimental mesocosms placed in the Chihuahuan dessert, while microcrustaceans were still missing (Walsh et al., 2014). In an earlier colonisation experiment with artificial freshwater pools, however, Holland & Jenkins (1998) collected only 10 rotifer and two microcrustacean species after 25 weeks, with only half of these species having arrived after 7 weeks despite the proximity of a permanent water body. In a quantitative study on the effective dispersal (colonisation) of newly constructed temporary ponds in Doñana National Park (Southern Spain), Frisch et al. (2012) showed that local environmental factors had no detectable effect on colonisation rates, while spatial factors (connectivity and location) and surface area were key determinants for colonisation by copepods and cladocerans, but not for rotifers. This suggests dispersal limitation in cladocerans and copepods, but not in rotifers, possibly due to differences in propagule size and abundance.

Besides different dimensions and shapes, dormant eggs sometimes also display a great variety of surface ornaments. In rotifers, for example, the egg surface can be smooth, rugose, with spiral ridges, floating chambers, labyrinth-like walls, hair-like projections, spines, spurs or flattened granules (Wurdak et al., 1978; Gilbert & Wurdak, 1978; Munuswamy et al., 1996; Walsh et al., 2016). A similar morphological variation is also revealed in large branchiopods (for a review see Brendonck & De Meester, 2003). This variation in shape and ornamentation of dormant stages has repeatedly been suggested to result in different dispersal rates, among other adaptations. Making use of a wind tunnel in a laboratory experiment, Pinceel et al. (2015) measured significant differences in dispersal propensity between dormant eggs of different shapes and sizes belonging to different species of branchiopod crustaceans on three distinct surface types. Larger propagules like cladoceran ephippia were lifted up more easily by the created airflow than smaller eggs, most likely since their shape facilitates aerodynamic lift. However, lift-off velocity does not provide information on whether the propagule is actually lifted to higher air-layers. In addition, propagules were more easily picked-up from a fine-grained surface than from a coarse grained or smooth one. This implies potential differences in lift-off from, for example, the smooth substrate of clay pans and the coarser sediment of rock pools. Another, often neglected, characteristic is the prevailing wind direction which has been shown to have an important role in channelling dispersal of cladocerans, copepods and rotifers along wind corridors (Hórvath et al., 2015).

Water connections between close-set pools in clusters are another important dispersal vector, at least at a local scale and for pools that overflow after heavy rainfall. Small pools with limited basin volume are expected to overflow more frequently than bigger pools with larger volumes, and as with wind dispersal may again function more as sources of dormant propagules than the receiving bigger pools (sinks). With abundant rains, large numbers of dispersing propagules were indeed collected at outflows of rock pools by means of overflow traps (Hulsmans et al., 2007; Vanschoenwinkel et al., 2008b). Especially the eggs of large branchiopods were well represented. This could be facilitated by the fact that a fraction of eggs float after rehydration of the pools (Hulsmans et al., 2007; Pinceel et al., 2013b). For pools that have a more central position in the cluster, this may result in successful dispersal, while floating eggs from marginal pools will be lost in the unfavourable terrestrial surroundings.

Some studies questioned the long-standing belief of zooplankton as frequent dispersers (e.g. Jenkins & Underwood, 1998; Bohonak & Jenkins, 2003). In this debate, it is especially important to define the spatial scale and to make a distinction between potential and realised dispersal (migration). Wind as a dispersal vector appears to be mainly important at a local scale (Brendonck & Riddoch, 1999; Cáceres & Soluk, 2002; Cohen & Shurin, 2003; Vanschoenwinkel et al., 2009), while it most likely loses relevance at a larger spatial scale, especially among distant and isolated water bodies. Juračka et al. (2016) described a pattern of decreasing likelihood of colonisation of ponds by cladocerans, copepods and ostracods, with an increasing degree of isolation. Vanschoenwinkel et al. (2008a) reconstructed dispersal kernels of the propagules of individual rock pool species and revealed a general decrease in dispersal rate with distance to the source for most taxa. Furthermore, dispersal rates usually already decreased drastically within 10 m from the nearest source (Vanschoenwinkel et al., 2009). Genetic studies confirm limited occurrence of effective dispersal over larger distances and suggest long distance dispersal only to occur at an evolutionary time-scale (Vanschoenwinkel et al., 2011; Pinceel et al., 2013c).

Impact on egg bank size

As not all dormant eggs hatch at the start of a growing season, a mixed (generations, genotypes, species) egg bank will develop of which the size and structure is dependent on hatching fractions, egg production during the aquatic phase, long-term viability of the dormant eggs, loss by wind erosion during the dry phase and by overflow during heavy rainfall (Brendonck & De Meester, 2003). The resulting egg bank will therefore be the budget of these gain and loss factors over seasons and years and contributes to the resilience (ecological memory) of populations and communities. Large pools of dormant stages have been documented from the active egg bank in all groups of freshwater zooplankton (see Brendonck & De Meester (2003) for a review). It was summarised that in zooplankton egg banks, egg densities usually range between 10^3 and 10^5 eggs per m^2, with densities up to 4×10^7 in rotifer egg banks. When losses overcome gain, the egg bank and buffering capacity can be eroded (Brendonck & Riddoch, 2000; Vanschoenwinkel et al., 2010a). The study of egg bank erosion is becoming increasingly relevant, since it may be impacted by anthropogenic alterations of the hydrology of pools (e.g. drainage, changes in depth and shape of the pool basin) and ongoing climate change. Based on global change models, for example, it is predicted that temporary pools in Australia will become dryer for longer periods (Nielsen et al., 2015). Simulations of changes in rainfall and evaporation for Southern Africa revealed that the proportion of successful inundations for a rock pool fairy shrimp species will decrease and that the length and frequency of dry periods will increase with predicted climate change (Hulsmans et al., 2008; Tuytens et al., 2014). This could enhance egg bank erosion in several ways. Firstly, if hatching fractions remain the same, an expected higher fraction of abortive hatching events will reduce egg bank sizes. In addition, during extended exposure of the dry egg bank, wind mediated erosion will increase (Graham & Wirth, 2008). Finally, dry sediments will be exposed to increased temperatures for longer time, which may reduce the future hatching ability of dormant eggs, and thus the resilience and biodiversity of temporary wetlands (Nielsen et al., 2015).

In the mainly obligatory sexual and oviparous large branchiopods, we expect the highest egg densities in pools with intermediate levels of hydrological disturbance (Table 2c) for two reasons. First, in highly ephemeral pools, disturbance may result in frequent abortive hatching and wind erosion events and hence an impoverished egg bank, while in ponds with long hydroperiods, predation pressure typically increases with time impoverishing the sensitive large branchiopod community (De Roeck et al., 2005; Waterkeyn et al., 2011). Second, the eggs of many species need several periods of drought to break dormancy (Brendonck, 1996). When the efficient filter feeding large branchiopods are present, cladocerans, rotifers and copepods are usually suppressed and population sizes small. In addition, these small-sized zooplankton groups first produce active offspring before switching to dormant egg production. We therefore expect no, or small, egg banks for these groups in ephemeral pools dominated by large branchiopods. Only in later phases of the pool hydrocycle, when large branchiopod populations decrease, can the micro-zooplankton community take over and start to produce dormant eggs. Theoretical, field and experimental evolution studies have reported an earlier switch to the production of dormant eggs in water fleas (Deng, 1997), rotifers (Carmona et al., 1995; Serra & King, 1999; Schröder et al., 2007, Gilbert & Dieguez, 2010, Campillo et al., 2011; Smith & Snell, 2012) and copepods (Hairston, 1996) in more disturbed habitats. Although this would suggest larger egg bank sizes in such habitats, clonal reproduction, on the other hand, can result in extremely large population sizes in habitats with long hydroperiods (De Meester et al., 2004). Therefore, once conditions deteriorate, a massive amount of dormant eggs could be produced and compensate for a continuous production of eggs during shorter hydroperiods as displayed in large branchiopods. Yet, if unfavourable periods are rare, the switch to the production of dormant eggs could be a sporadic event and the egg bank could be poorly developed.

Finally, besides depending on the interplay between species traits and hydroregime, egg bank dynamics and the egg bank size also depend on other factors such as plant cover. Brendonck and Riddoch (2000), for example, illustrated that egg bank erosion in Botswana rock pools was more significant in shallow pools that were not protected by vegetation. Also Vanschoenwinkel et al. (2010a) counted higher egg densities in the sediments of plant covered pools in contrast to entirely open ones. However, the presence of plants can sometimes be independent of the level of hydrological disturbance. Therefore, the presence or absence of plants could also obscure a direct relationship between the pool hydrology and egg bank size.

Impact on population structure

Depending on the hatching fraction from the mixed persistent egg bank, the long-term viability of eggs and the intensity of sediment mixing (Brendonck & De Meester, 2003; Ortells et al., 2005), the resulting generation overlap has strong demographic and genetic consequences. From a demographic perspective, it changes the age-structure of populations and increases effective population sizes (Evans & Dennehy, 2005). From a genetic angle, the archiving of genotypes over time serves to maintain genetic diversity (Ellner & Hairston 1994; Hedrick, 1995; Hairston et al., 1996; Ortells et al., 2000), which facilitates responses to environmental change (Hairston, 1996). Moreover, gene flow among temporally distant populations through delayed hatching can enhance or delay micro-evolutionary processes depending on the strength and direction of selection, the effective population size and the level of generation overlap (Templeton & Levin, 1979; Hairston & De Stasio, 1988; Ellner et al., 1999; Hairston et al., 1999). In addition, rapid build-up of an egg bank by the first colonisers in a population may, through founder effects, reduce chances of other genotypes to establish. Founder effects and resource monopolisation could explain the contra-intuitively high genetic differentiation among neighbouring zooplankton populations (De Meester et al., 2002). This has been observed in *Daphnia magna* Strauss, 1820 colonising new ponds in Spain (Ortells et al., 2012) and Belgium (Ortells et al., 2014).

The relative importance of the above processes and the impact of mixed resting egg banks on genetic diversity within and genetic differentiation among populations are expected to differ along a gradient of hydrological disturbance. The highest local diversity and lowest among population differentiation are expected at intermediate levels of disturbance (Table 2c). Genetic diversity has been mostly associated to pond size or age in cladocerans (Michels et al., 2003; Vanoverbeke et al., 2007; Haag et al., 2005), large branchiopods (Riddoch et al., 1994; Brendonck et al., 2000; Naihong et al., 2000; Bohonak, 1998; Hulsmans et al., 2007) and rotifers (Montero-Pau et al., 2016). It has only recently also been studied in relation to hydrological stability (Walser & Haag, 2012). These authors compared populations of *D. magna* from small rock pools with strong population turnover with those from medium sized more stable ponds and found strongly reduced levels of genetic diversity in the highly disturbed rock pools. Furthermore, high turnover dynamics prevented frequent gene flow, increasing genetic drift and genetic bottlenecks, resulting in decreased genetic diversity, inbreeding and increased differentiation among subpopulations (Haag et al., 2005, 2006). In addition, also the buffering capacity of the egg bank is expected to be reduced in ephemeral systems due to their smaller egg bank size. The resulting stochasticity of a reduced hatching fraction in response to habitat predictability in these types of habitats should further increase genetic drift and differentiation (Schwentner & Richter, 2015).

The above patterns may differ depending on chance and species: genotype characteristics and may be highly dynamic in time. In new habitats, for example, first founders may exert persistent effects through the build-up of an egg bank and largely determine the genetic structure of the population (Boileau et al., 1992; De Meester et al., 2002; Gómez et al., 2002; Thielsch et al., 2015). With time, original founder effects can be eroded by subsequent gene flow if immigrants have a selective advantage over highly inbred local residents, an effect experimentally demonstrated in the cladoceran *D. magna* by Ebert et al. (2002) and in the rotifer *Brachionus plicatilis* Müller, 1786 by Tortajada et al. (2010). Due to limited time for dominant species to take over by the frequent turnover, we expect founder effects to persist longer in more frequently disturbed pools. In well-established habitats, the growing season usually starts with a variable number of genotypes at the moment of initial hatching from the egg bank. Eventually, genetic diversity is eroded along the planktonic period if selection is strong and directional, and the growing season is long enough (Gómez & Carvalho, 2000; Pálsson, 2001; De Meester et al., 2006; Ortells et al., 2006). Such genetic erosion has important consequences for genetic diversity and genetic differentiation in relation to hydrological disturbance (Table 2c). In addition, in highly disturbed habitats, early produced dormant eggs by zooplankton should be more genetically diverse than those produced at the end of the growing season in less disturbed pools. In turn, genetic differentiation is expected to be maximum among ponds with a long and stable hydroperiod due to local adaptation aided by a large dormant egg bank (Table 2c).

There will also be differences among organism groups in genetic structuring because of variations in their life cycle and reproduction strategies. For example, due to clonal reproduction during at least part of their life cycle, it is expected that founder effects after colonisation will be more likely in rotifers and daphnids than in sexually reproducing large branchiopods that will need many founding eggs for a healthy population to establish. Similarly, the erosion of genetic variability should be stronger in cyclical parthenogenetic organisms in comparison with obligately sexual organisms, as selection in the water phase efficiently eliminates whole genomes (De Meester, 1996).

Impact on community structure

Ebert & Balko (1987) extended the island theory by MacArthur & Wilson (1967) to the temporal scale of temporary ponds by including duration and frequency of flooding (hence hydrological disturbance regime) as predictors of immigration and extinction rates of the pool inhabitants. According to theoretical predictions and analogous to the island theory, taxon richness should increase when more niches become available as the inundation progresses and heterogeneity increases. As such, temporary pools are considered as island in time and space (Williams, 2006). The length of the inundation period (i.e. hydroperiod), as an important component of the hydrological disturbance gradient, is generally recognised as an important structuring factor of invertebrate communities in temporary pools (Schneider & Frost, 1996; Wellborn et al., 1996; Boven and Brendonck, 2009). In pools with a relatively long hydroperiod, indeed more time is available for community development and a gradual occupation of niches, resulting in a higher probability for successful colonisation and recruitment by a more diverse set of taxa (Baber et al., 2004; Tavernini et al. 2005; Waterkeyn et al., 2008). For example, different types of food resources that become available throughout the season enable the succession of detritivore, herbivore and predatory species (Meintjes, 1996; Lahr et al., 1999; Boven et al., 2008), while the developing aquatic vegetation creates suitable microhabitats for plant-associated zooplankton species that gradually replace planktonic species (Hann & Zrum, 1997).

The gradual changes in the invertebrate communities during the hydroperiod of temporary pools are sometimes used to distinguish successional stages (filling, intermediate and drying phases) in the pond cycle (e.g. Sahuquillo & Miracle, 2010). As the hydroperiod shortens, some successional stages may be truncated (Boix et al., 2004), a phenomenon that was used by Jocqué et al. (2007) to define ephemeral ponds. In a newly flooded habitat (filling phase), permanent residents typically appear first. They survive the dry period as dormant propagules (e.g. cladocerans, large branchiopods, copepods, rotifers) or other drought-resistant life stages (e.g. snails, chironomids, some beetles and odonates) (Wiggins et al., 1980). The recolonisation after filling generally results in an increase in taxon richness over time (Lake et al., 1989; Bazzanti et al., 1996; Boix et al., 2004, Culioli et al., 2006; Jocqué et al., 2007). After some time, taxon richness may reach a plateau when a continuous turnover or replacement of taxa occurs (Lake et al., 1989) and niche saturation is possibly accomplished. During the ‘intermediate’ and ‘drying’ pool phases, actively dispersing insects (odonates, bugs and beetles) arrive from permanent or other temporary habitats (Wiggins et al., 1980), increasing the predation pressure on early colonisers. In South African and Australian temporary rock pools, for instance, large zooplankters (such as large branchiopods) hatch fast and dominate early successional stages, only followed later by smaller cladoceran grazers (Jocqué et al., 2010; Vanschoenwinkel et al., 2010b). Whereas some predatory species, especially turbellarians, are already present during early stages of the inundation, major predators such as insects

(Hemiptera and Coleoptera) typically only colonise ponds if hydroperiods are long (Vanschoenwinkel et al., 2010b). In the drying phase of the ponds, only the most opportunistic and resistant species remain, which are able to cope with a deteriorating environment. Therefore, a drop in taxon richness often occurs before desiccation as various taxa leave the habitat due to harsh abiotic conditions or more intense predation (Bazzanti et al., 1996; Lahr et al., 1999). Several studies suggest that communities from stable ponds with long hydroperiods are primarily structured by biotic interactions that act as a strong filter (Nakazawa et al., 2011; Nielsen et al., 2013) as idealised in Table 2b. In contrast, communities from pools with high levels of disturbance and predictability of suitable growing conditions are highly constrained by their physical environment (Schneider & Frost, 1996; Allen et al., 2011; Vanschoenwinkel et al., 2013; Brendonck et al., 2015; see Table 2a).

Prolonged inundations also facilitate a greater diversity of conditions enabling the hatching of more species from dormant eggs (Antón-Pardo & Armengol, 2010). With extended hydroperiods, chances also increase for dispersal events to be successful, in contrast to ephemeral pools that will be in the dry state for a major part of the year. But even in pools with limited hydrological disturbance, local conditions may be unsuitable for newly arriving propagules to hatch or for hatchlings to develop in sufficient numbers to a mature stage.

For most of the above processes, there is empirical evidence from field studies. It remains, however, to be confirmed to what extant patterns revealed with specific study systems and taxa can be generalised to other types of temporary water systems and organism groups. Taking also the described egg bank processes in consideration, maximum species numbers are expected in ponds with intermediate disturbance, with a decrease in species richness towards the ephemeral and more stable end of the disturbance gradient (i.e. near-permanent and predictable) (Table 2c). Serrano & Fahd (2005) found an overall positive effect of hydroperiod on community richness in freshwater temporary ponds of the Donana National Park (SW Spain). Making use of the same study system, Florencio et al. (2015) showed that species turnover rates in the microcrustacean communities were especially high, early in the inundation of short lived ponds, while nestedness increased in all ponds types during later pool phases. The species richness of copepods and large branchiopods was highest in intermediate-hydroperiod ponds, which harboured a large number of common species, while rare species were more abundant in ponds of a short hydroperiod. Assemblage dissimilarities were particularly high among ponds just after the initial filling phase, probably because of the restrictive requirements governing the hatching of microcrustacean species. In temporary pools with variable hydroperiod in the Kiskunság National Park (Hungary), initial communities did not differ among pools with different inundation regimes, but species turnover took place in later phases of the pool cycle in medium and long hydroperiod pools, probably due to predation and the development of plants (Boven et al., 2008). Cumulative species richness also increased with hydroperiod length. During a 4-year study since the moment of restoration, a temporary peridunal pond in Eastern Spain was first colonised by rotifers, followed by copepods. Cladocerans and ostracods gained importance in the second year, when the first sprouts of helophytes and macrophytes were detected (Olmo et al., 2016). In the whole set of peridunal ponds with different hydroperiod lengths occurring in the same area, ponds with shorter inundations were richer in organisms of short life cycles like rotifers, while species richness was positively associated with hydroperiod length. Nielsen et al. (2013) found experimental evidence of reduced biotic diversity in plants and micro fauna emerging from sediment of Australian temporary wetlands that were hydrologically more stable (either more permanently dry or more permanently wet).

The relation between pond disturbance and taxon richness is, however, not always straightforward as it can differ among taxon groups and due to interactions with other factors. Serrano & Fahd (2005) found that only a limited number of cladoceran and rotifer species were restricted to pools with a specific hydroperiod in the Donana National Park (SW Spain). In a temporary pond of northeastern Spain, Boix et al. (2001) in turn, found a significant correlation between the length of the hydroperiod and taxon richness of macroinvertebrates but not of microcrustaceans. Hydroperiod alone might indeed not always explain zooplankton taxon richness, as a longer hydroperiod is often accompanied by temporal variation in other environmental factors (Serrano & Fahd, 2005). Both changes in abiotic (conductivity, water level, temperature) and biotic conditions (competition, predation and facilitation) interactively shape community dynamics during the successive phases of a pool cycle. In Spanish temporary ponds, community changes during early, middle and late inundation phases were related to availability of food sources, biotic interactions and temperature increases, respectively (Boix et al., 2004). Further in this respect, Waterkeyn et al. (2008) found significant individual and interacting effects of hydroperiod (positive) and salinity (negative) on invertebrate taxon composition in Camargue temporary ponds.

Other studies suggest an interaction between local hydrological disturbance and spatial factors (e.g. isolation) in explaining community composition (Table 2a). In a study on South African rock pools, Vanschoenwinkel et al. (2013) showed that hydrological disturbance had the strongest impact on species diversity in isolated pools, which, consequently, had lower alpha diversity than pools that were set closer together. Rare long-range dispersal apparently does generally not allow for recolonisation of pools with short and variable hydroperiods where local population crashes may be frequent (see dispersal and colonisation processes above). Yet, when pools are close to each other, effective short range dispersal (e.g. by water connections or wind) provides a large propagule pool for effective lineage sorting. In addition, high dispersal levels may sustain species and genotypes that are maladapted to the prevailing conditions through mass effects (Urban, 2006). Nearby and neighbouring rock pool communities, for example, were more similar than would be expected based on similarities in environmental conditions (Vanschoenwinkel et al., 2007). Using a set of invertebrate communities from rock pool clusters along a latitudinal gradient in Western Australia, Brendonck et al. (2015) investigated the importance of hydrological disturbance for explaining both local and regional diversity patterns and revealed that Hydrological stability was strongly positively associated with local alpha (local scale) and gamma diversity (regional scale).

When environmental conditions are temporally variable and favour different species at different moments, and if dormant eggs survive long enough to bridge unfavourable periods, storage effects can facilitate species coexistence (Chesson, 1983; Cáceres, 1997b). The same process similarly impacts the coexistence of genotypes and may hence result in higher genetic and species diversity than what is predicted by traditional models and is predicted to be highest at intermediate levels of disturbance (Table 2c). Coexistence mediated by the storage effect has been reported in predator–prey or strong competition dynamics in copepods, cladocerans and rotifers (Hairston, 1996; Brendonck & De Meester, 2003; Montero-Pau & Serra, 2011; Wang et al., 2011; Aránguiz-Acuña & Ramos-Jiliberto, 2014). Habitat predictability and variable diapause investment can also affect the competitive dynamics between generalists and specialists (Franch-Grass et al., 2014). For example, the rotifers *Brachionus plicatilis* and *B. manjavacas* Fontaneto et al., 2007 are two cryptic species with a considerable ecological overlap that historically co-occur in highly unpredictable and fluctuating brackish ponds (Fontaneto et al., 2007; Montero-Pau et al., 2011; Gabaldón et al., 2013). Coexistence is possible because the specialist *B. plicatilis* invests in diapause during ephemeral and favourable conditions (low salinity) which accelerates its exclusion from the water column but promotes long-term persistence (Gabaldón et al., 2015). On the other hand, the more generalist *B. manjavacas* has a density dependent diapause investment that favours inferior competitors (Montero-Pau & Serra, 2011).

Final remarks

Our review deals with different environments and taxa at an obvious trade-off with resolution. An improved understanding of how hydrological disturbance moulds zooplankton population and community processes is an essential step in the development of a unified conservation and management strategy of temporary pools. Especially dormancy and dispersal characteristics are of great importance for the long-term persistence of resident (meta)populations and (meta)communities. These characteristics are partly determined by the hydrological disturbance and spatial configuration of pools, which are directly impacted by anthropogenic disturbance and climate change. Due to habitat loss and continued fragmentation, the distance between pools in a metacommunity setting is increasing and efficient dispersal is becoming limiting. Precisely in such environments, the disturbance caused by sequences of drought spells may ultimately lead to local crashes of the most sensitive populations. In addition, any direct (e.g. drainage, deepening, filling) and indirect (e.g. climate change) anthropogenic impact on the hydrology of temporary pools might have drastic effects on structure and functioning of their populations and communities.

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