Conservation of Temporary Wetlands

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Abstract

Temporary wetlands are characterized by frequent drying resulting in a unique, highly specialized assemblage of often rare or specialized plant and animal species. They are found on all continents and in a variety of landscape settings. Although accurate estimates of the abundance of temporary wetlands are available in only a few countries, global estimations identify a decline in number and quality. The key environmental factors driving the structure of ecological communities in temporary wetlands are the duration, timing, frequency and predictability of the aquatic and dry phases, which varies greatly with region and hydrogeomorphic setting. Temporary wetlands have been historically neglected, but improved social awareness of the functions and values of, and increases in scientific interest, suggest that this is changing. They play an ecological role in both global cycles (i.e., CO_2 emissions) and biodiversity (in proportion to their size, they contribute disproportionately to regional and global biodiversity). Moreover, they provide valuable ecosystem services including wildlife habitat, nutrient flux to adjacent ecosystems, flood control, water filtration, and cultural services. Effective conservation of temporary wetlands requires addressing threats (i.e., inconsistent and inadequate regulatory protections; climate change; changes in land use) and management challenges (i.e., management at both local and landscape scales; incomplete understanding of the ecosystem services provided by them; the need to enhance inventories). The most suitable approaches for conserving temporary wetlands include (1) regulations or other forms of protection; (2) sustainable management; (3) restoration and creation; and (4) collaborative conservation.

What Are Temporary Wetlands?

Temporary wetlands are wetlands characterized by frequent drying (normally they dry completely, at least, once a year) resulting in a unique, highly specialized assemblage of often rare plant and animal species (Calhoun et al., 2017). Their defining feature is hydroregime (duration, timing, frequency and predictability of the aquatic phase; Vanschoenwinkel et al., 2009; Sim et al., 2013), and, in some regions, the cyclical nature of droughts, as some permanent water bodies may dry in exceptional years (Williams, 2006). While throughout our discussion we refer to these landscape features as "temporary wetlands," it is only the ponded water in the wetland that is temporary in nature. The wetlands themselves are persistent features of a landscape that exist unless drained or filled (Van der Kamp et al., 2016). Usually the water turnover rate is considered the primary environmental cue used to identify the different types of freshwaters ecosystems (Margalef, 1983; Wetzel, 2001). Thus, wetlands with short turnover periods (i.e., lotic environments; streams and rivers) differ in both function and community structure than those with longer turnover periods (i.e., lentic environments; wetlands). Hydroregime is the main environmental indicator of gradients in lentic environments (Schneider and Frost, 1996; Wellborn et al., 1996). Hydroregime not only implies physical and biogeochemical changes (especially carbon cycling) in the habitat, but also drives ecological interactions by shaping food webs and altering the composition of potential competitors and predators of species previously adapted to temporary water regimes (Williams, 2006; Lake, 2011).

Where Are Temporary Wetlands Found?

Temporary wetlands are found on all continents, even in Antarctica (Antarctic melt-water ponds), and in a variety of landscape settings, although temporary wetlands exhibit regional differences because different typologies are especially abundant in some areas (Fig. 1) (Zedler, 2003; Williams, 2006; Calhoun et al., 2017). Temporary wetlands are important features in landscapes where permanent water sources are rare (i.e., semiarid and arid areas; Williams, 1985). Many of these wetland features were recognized by ancient cultures and are still considered a valuable part of regional heritage. For example, Aristotle described the biological functioning of one Mediterranean temporary wetland in his "History of Animals" (Boix et al., 2016); Australian Aboriginal people shared knowledge passed down from generation to generation with Europeans about the temporary "gnamma" holes, which were one of their main sources of water (they even elaborated a technique to deepen them) (Bayly, 1999). In addition, temporary wetlands have been created in Europe by humans at least since Roman and Gallo-Roman times as agricultural ponds (Derex, 2001; Delhoofs et al., 2010). Deliberate wetland creation (for runoff and flooding abatement or as incidental features from forestry or development practices) are still common today (Calhoun et al., 2014a).

Estimates of the location, surface area, abundance, and relative importance of temporary wetlands are available in only a few countries and often only for some regions. However, a global estimation shows that in a contemporary timeframe (i.e., 2015), seasonal water covered 0.81 million km^2, and in the last three decades the transition from permanent to seasonal waters was higher than the reverse transition (72,000 km^2 and 29,000 km^2, respectively) (Pekel et al., 2016). In some areas, shifts to more permanent water regimes have occurred, either through the drainage of many smaller wetlands into fewer larger wetlands, which is known as "consolidation drainage" (McCauley et al., 2015); through the construction of dugouts or dikes in wetland basins (Euliss and Mushet, 2004); or through increases in timing and intensity of rainfall events as a result of changing climate regimes (McKenna et al., 2017).

Because they are temporary and generally small, temporary wetlands can be challenging to identify using remote-sensing techniques. Advances in technology, including light detection and ranging (LiDAR), can improve global inventories of temporary wetlands (e.g., Gómez-Rodríguez et al., 2010; Rhazi et al., 2012; Tulbure et al., 2014; Wu et al., 2014). This knowledge is crucial for evaluating their number, distribution, and perhaps increasing their value to society (small waterbodies have been poorly inventoried and undervalued; Downing et al., 2006); and to track widely reported losses (e.g., Brown, 1998; Euliss and Mushet, 1999; Rhazi et al., 2012). Although auditing the numbers and size of wetlands remains a challenge (Jeffries et al., 2016), global estimations identify a negative trend. Since the beginning of the 18th century, wetland loss (mainly inland, temporary wetlands) could have been greater than 80% and wetland loss in the 20th century was almost four times faster (Davidson, 2014). For this reason, the functions and values of temporary wetlands need to be acknowledged and better understood.

Diversity of Temporary Wetland Physical Attributes

Most lentic temporary environments can be considered temporary wetlands, with the exception of some unique habitats (e.g., phytotelmata, a small water-filled cavity in a terrestrial plant). Temporary wetlands are globally distributed and shaped by distinct climate conditions in a variety of biomes and thus encompass a wide range of attributes (Williams, 1985; Williams et al., 2010). For example, although temporary wetlands are generally shallow and relatively small, they vary in (1) size (from a few square centimeters of some rock-pools to hundreds of square kilometers of North American "playas" or thousands of square kilometers of ephemeral Australian lakes), (2) substrate (rock, sand, clay), (3) hydroregime (from ephemeral water bodies in arid regions to seasonal ponds in temperate zones), and (4) sources of water input (rain, snowmelt, stream flow, subterranean). Thus, although rain provides the main water input to temporary wetlands in a great number of regions, in others snowmelt or subterranean waters can play this role (e.g., Irish "turloughs") and be a determinant of long-term changes in wetland permanence (LaBaugh et al., 2018). Therefore, temporary wetlands comprise a wide range of worldwide waterbody types (Fig. 1), resulting in diverse names to describe them (Williams, 2006; Williams et al., 2010; Calhoun et al., 2017).

Fig. 1 Examples of temporary wetlands (clockwise from top *left*): Gilgais amongst Plains Grassy Woodland, Monea North Nature Conservation Reserve, Victoria, Australia (photo: J. Fitzsimons); Alpine seasonal pools, Val Thorens, alt. 2520 m, French Alps (photo: F. Isselin-Nondedeu); small rock pool, Massif Central alt. 1500 m, Parc Naturel Régional des Volcans d'Auvergne, France (photo: F. Isselin-Nondedeu); Mediterranean temporary pond, Albera piedmont, Catalonia, Spain (photo: A. Ruhí); dry vernal pool, Acadia National Park, Maine, United States (photo: A. Calhoun); Great Plains prairie pothole, North Dakota, United States (photo: D. Mushet).

Key Environmental Variables and Classification of Temporary Wetlands

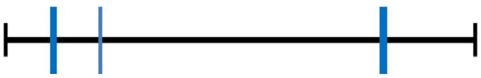
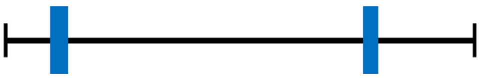
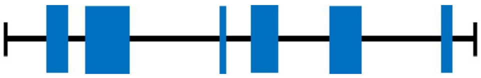
The key environmental factor driving the structure of ecological communities in temporary wetlands is hydroregime. Hydroperiod length or pond duration is the most studied hydrologic component, in large part due to its influence over community dynamics and structure (Sim et al., 2013; Boix and Batzer, 2016). However, other aspects of hydroperiod also play a key role, such as predictability (Comín and Williams, 1994) or inundation timing (Kneitel, 2014). Interactions between hydroregime and various biological factors (i.e., predation pressure, strategies to resist desiccation or to recolonize rapidly) have been documented (Wellborn et al., 1996; Jeffries et al., 2016). These interactions can be complex and difficult to predict, complicating identification of general patterns of how organisms will respond to hydroregimes (Batzer, 2013), a fact that contributes to the diversity of temporary wetlands.

Pond size is also considered a determinant factor for many features of temporary wetlands although this varies by region (e.g., Ebert and Balko, 1987; March and Bass, 1995; Meintjes, 1996; Spencer et al., 1999). Overall, indirect effects of pond size on community structure (i.e., larger ponds have different environmental characteristics than smaller ponds) seems to be weak in temporary ponds (Ballón et al., 2016). However, in forests, pond size may be correlated with tree canopy closure in some regions, which influences quantity of photosynthetic active radiation and inputs of organic matter consequently structuring part of ecosystem functioning (Mokany et al., 2008; Skelly et al., 2014). Moreover, the interaction of both factors, hydroregime and pool size, has been related to some ecological traits such as the dispersion of the taxa (Vanschoenwinkel et al., 2009).

Several methods for classifying temporary wetlands have been attempted including classification by the biome in which they are present (e.g., tundra, temperate grassland, Mediterranean scrub, tropical savanna), size (i.e., micro-, meso-, macro-habitats), hydrological character (i.e., intermittent, episodic), salinity (i.e., freshwater, saline), origin (natural, artificial; and the latter can be classified according to human use), indicator species, or a combination of several of these factors (Williams, 1985, 2006; Rheinhardt et al., 2008). Classifications based on hydrology, including duration and predictability of the hydroperiod, are frequently used (Comín and Williams 1994; Keeley and Zedler 1998). This includes the most widely accepted classification of temporary wetlands, proposed by Boulton and Brock (1999), which has been adapted and reproduced in several ecology textbooks (e.g., Boulton et al. 2014; Grillas et al., 2004; Williams, 2006; Boix et al., 2016). The classification distinguishes five types of temporary lentic waters (Table 1). These temporary wetlands types are related by potential future changes of hydroregime. Thus, trends of precipitation variation (increases or decreases, which are regionally dependent) and increase of extreme events (such as heavy precipitation events or long dry periods) predicted in accordance with climate change (Brooks 2009; Stocker et al., 2013) imply possible transitions among the separate types of temporary wetlands (Fig. 2).

The relevance of hydrology in shaping ecological function of temporary wetlands is also the core of the conceptual framework of the "Wetland Continuum" (Euliss et al., 2004). This conceptual framework is more comprehensive than the scenarios illustrated in Fig. 2 because it includes not only precipitation but also groundwater recharge or discharge, facilitating the interpretation of biological studies of wetland ecosystems (Mushet et al., 2018). The objective of the Wetland Continuum framework is "to provide a

Table 1 Classification of temporary wetlands (TW) according to their hydroregime with some comments of the characteristics of the organisms living in them.

TW type	*Flooding regime*	*Hydroregime*	*Organisms*
Ephemeral		Filled only after unpredictable rain and by run-off. The flooded area dries out during the days following the flooding	Supports low numbers of macroscopic aquatic species compared to pools with longer hydroperiods
Episodic		Dries in 9 out of 10 years, with rare and irregular flooding (or wet periods) which may last for a few months	Terrestrial flora with few aquatic species. Fauna characteristic of temporary waters, dominated by species with highest dispersion capacity or drought resistant strategies
Intermittent		Alternating wet and dry periods, but a more irregular frequency of filling than seasonal wetlands. Flooding may persist for months or years	Aquatic flora restricted to the inner belt. Fauna characteristic of temporary waters, but also species that use waterbody as breeding or feeding site
Seasonal		Alternating wet and dry periods annually, in accordance with the season. Usually fill during the wet season of the year, and dry out in a predictable way every year	Since flooding lasts for several months, macroscopic animals and plants are able to complete their life cycles
Near-permanent		Predictable flooding, though water levels may vary. The annual input of water is greater than the losses (does not dry out) in 9 out of 10 years	The majority of organisms living here cannot tolerate desiccation
	 10 years		

Adapted from Boulton, A.J. and Brock M.A. (1999). *Australian freshwater ecology: Processes and management*. Canberra, Cooperative Research Center for Freshwater Ecology.

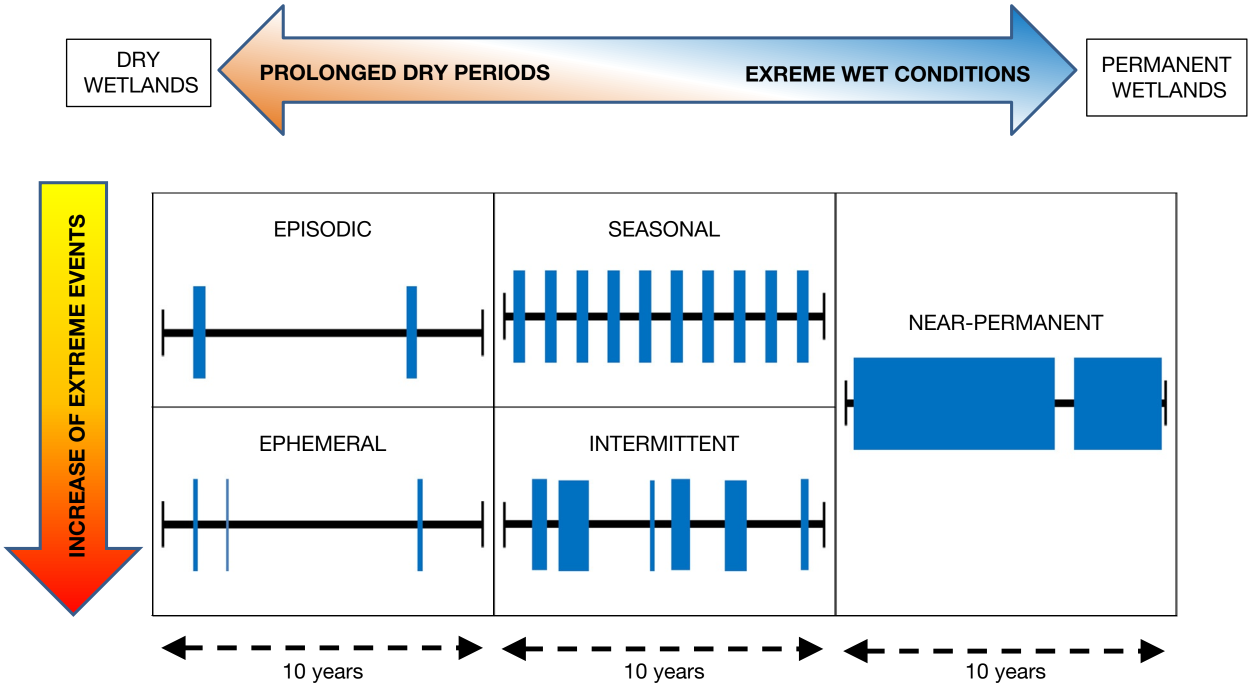


Fig. 2 Changes among temporary wetland types (according their hydroregime, see Table 1) in some future climate scenarios (Stocker et al., 2013) taking into account two aspects: variation in precipitation and increase of extreme events (i.e., heavy precipitation events or long dry periods).

method that can be used to complement existing classification systems by placing dynamic shifts in wetland class and function within an ecological context to improve interpretation among biological studies conducted in different locales and times." This method is also a powerful tool for analyzing future changes in ecological functioning due to periods of wet or dry conditions (Mushet et al., 2018). Exemplary situations to which the Wetland Continuum framework may be applied include the Prairie Pothole Region of North America, which has been subjected to an extended period of extreme wet conditions (McKenna et al., 2017); or the substantial decline of annual rainfall observed since 1900 in several Mediterranean regions owing to climate change (IPCC, 2007) with markedly prolonged dry periods in wetlands. These hydrological changes imply potential modifications in the populations and metacommunities dynamics, and different patterns between organisms with different dispersion mode or ability are expected (Pyke, 2005; Sim et al., 2013; Boix et al., 2016).

The Age of Enlightenment for Temporary Wetlands? From Negative Perception to Valued Resource

The conservation status of many temporary wetlands around the world is attributable to a long-held negative perception of temporary wetlands. As mentioned earlier, while some ancient cultures in arid and semiarid regions had historic knowledge of temporary wetlands and valued them as part of their heritage, in modern societies these same wetlands are generally viewed more as wasteland or a liability (e.g., as sources of diseases or undesirable animals such as mosquitoes, or a loss of agriculture or developable land) than as valuable assets (Batzer and Boix, 2016; Jeffries et al., 2016). Moreover, the ecological value of individual temporary wetlands has increased as conversion of wetlands to other land uses has increased their rarity in the landscape. Additionally, temporary wetlands have historically received limited scientific attention and, even in some cases, perceptions of the ecology of these habitats are incorrect as conclusions were not evidence-based but rather were extrapolated from studies on permanent wetlands and wetlands in other climates, or were directly compared to permanent wetlands. Despite this, evidence to date suggests that temporary wetlands, by nature of their unique environmental conditions, contribute to beta and gamma diversity (Williams, 2000; Boix et al., 2008; Calhoun et al., 2017). To further complicate our understanding of this system, some scientific ideas on how temporary wetlands function had been established without direct documentation. Results from direct study of temporary wetlands open the door to a different perspective: predation could be an important biotic driver for community structure (Brendonck et al., 2002; Boix et al., 2006; McLean et al., 2016); drought is not a determinant environmental filter in all temporary wetlands because many species are adapted to drought (Biggs et al., 1994; Williams, 1996); and hydroperiod duration is not always the main hydrological factor to explain community composition, because in Mediterranean regions flooding timing could play a more determinant role (Kneitel, 2014; Boix et al., 2016).

Peer-reviewed literature on temporary wetlands is limited prior to the mid-twentieth century (Williams, 2006; Grillas et al., 2010; Jeffries et al., 2016). Using the words of Prof. William D. Williams (1985), "Despite the obvious ubiquity, ecological importance and limnological interest of temporary waters, most limnological texts have little to say about them". In fact, for this reason Prof. D. Dudley Williams named temporary wetlands as "the Cinderellas of aquatic science"—in other words, the ugly and neglected little sister of the more charismatic, larger wetlands (Williams, 2006). However, an increase in scientific interest of temporary wetlands is evident for the following reasons (Blaustein and Schwartz, 2001; Williams, 2006):

- temporary wetlands are ubiquitous and many of them small, making them ideal subjects for pure and applied research studies;
- temporary wetlands can support a wide range of studies because they can be more readily manipulated for experiments, and their abundance allows for replication;
- temporary wetlands contribute to general understanding of "ephemerality" phenomena in terms of ecosystem functioning, community structure, and population dynamics of biological adaptations;
- temporary wetlands are inland environments characterized by high physical variability, and this variability drives both molecular and morphological evolution;
- temporary wetlands harbor disease vectors;
- temporary wetlands significantly contribute to aquatic biodiversity;
- temporary wetlands contain an important proportion of land-water ecotone;
- temporary wetlands have played a key role in biogeographical processes, because they served as postglacial dispersal routes.

Other investigators have noted additional wetland contributions of scientific importance, which include the following:

- temporary wetlands could be important study systems for explaining the origins of life, as earliest life forms may have arisen in shallow ponds (Ranjan et al., 2019);
- temporary wetlands represent an example of faunal complexes persisting over millennia with locally adapted endemic species (Keeley and Zedler, 1998);
- temporary wetlands are characterized by a unique combination of isolation and connectedness at different spatial scales, which can result in the evolution of endemic species (Zedler, 2003);
- temporary wetlands play a significant role in global cycles (Downing, 2010; Obrador et al., 2018), especially in C cycling through C storage and through emitting CO_2 (Holgerson, 2015; Holgerson and Raymond, 2016; Marcé et al., 2019); and
- temporary wetlands are an ideal habitat to study metacommunity dynamics because they configure networks of aquatic patches inside a terrestrial matrix with a reduced time window for species dispersal (Jeffries et al., 2016; Tornero et al., 2018; Cunillera-Montcusí et al., 2019).

Improved social awareness of the functions and values of and increases in scientific interest in temporary wetlands suggest perceptions of this resource are changing (Angeler, 2009; Brock, 2009; Calhoun et al., 2014b). The latter is demonstrated by the rising number of publications as journal articles (Fig. 3), monographs or proceedings of workshops or symposia (e.g., Diget and Rioux, 1998; Witham, 1998; Blaustein and Schwartz, 2001; Fraga, 2009; Bagella et al., 2016), and textbooks or chapters on

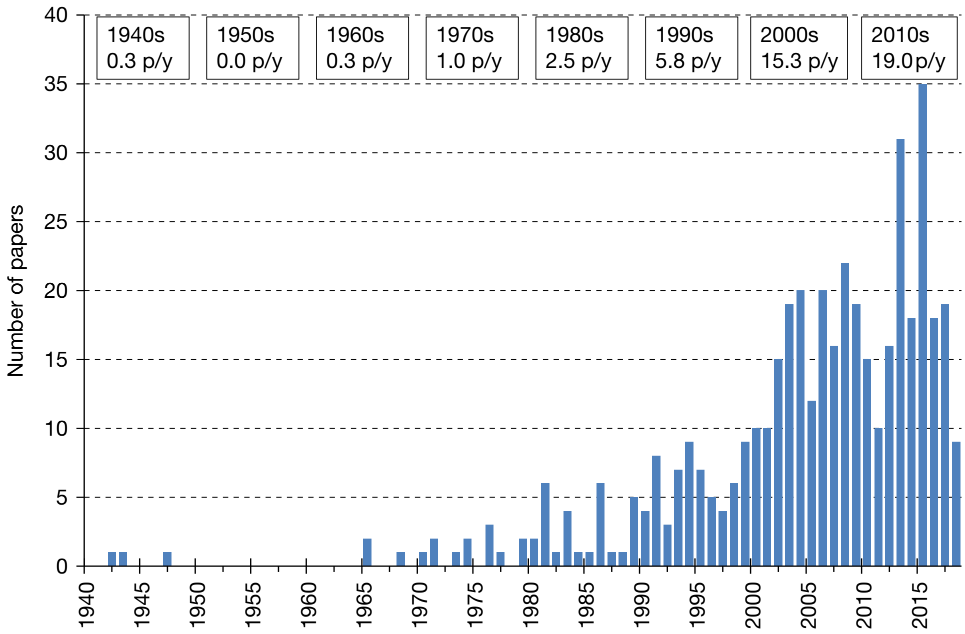


Fig. 3 Number of papers published every year (p/y) from 1940 to 2019 in which the following terms are included in the title: "temporary wetlands," "temporary ponds," "temporary pools," "ephemeral wetlands," "ephemeral ponds," "ephemeral pools," "vernal ponds," and "vernal pools". Data extracted in July 2019 from the data base "Web of Science" (Clarivate Analytics). The top boxes show the mean number of publications per year for each decade.

temporary wetland ecology (e.g., Williams, 2006; Alfonso et al., 2011; Lake, 2011; Boix et al., 2016; Jeffries et al., 2016) or conservation (e.g., Grillas et al., 2004; Calhoun and deMaynadier, 2004, 2008; Fraga et al., 2010; Sancho and Lacomba, 2010; Díaz-Paniagua, 2015).

Why Are Temporary Wetlands Ecologically and Socially Important?

Biogeochemistry and Hydrology

Gaps in our knowledge about the distribution and abundance of small waterbodies, or temporary wetlands, have been long neglected (Downing et al., 2006), and not surprisingly, so has the role of these wetlands in global cycling of matter (Downing, 2010; Hunter et al., 2017; Golden et al. 2019). Part of this can be explained by the relatively small size of most temporary wetlands, but their neglect can also be explained by the temporary nature of their ponds, making the wetlands themselves perceived as being temporary landscape features (Grillas et al., 2004; Boix et al., 2016; Van der Kamp et al., 2016). Ironically, it is this very characteristic of alternation between dry and wet phases of temporary wetlands that makes them crucial biogeochemical hotspots compared to surrounding upland systems. For example, dry wetlands substantially contribute to CO_2 emissions and have long been known as sources of CO_2, whereas inundated wetlands acted either as a source or a sink of atmospheric CO_2 (Catalán et al., 2014; Holgerson, 2015; Obrador et al., 2018). These CO_2 emissions have only recently been included in global estimates of CO_2; the first published estimates reveal a significant contribution of temporary systems (Marcé et al., 2019). Other biogeochemical functions of temporary wetlands include denitrification, sediment retention, pesticide transformation, and absorption of phosphorus and other aquatic pollutants (Zeng and Arnold, 2013). Temporary wetlands provide a disproportionately large fraction of wetland edges, and biogeochemical and other wetland functions tend to be enhanced in areas of wetland-edge (Cohen et al., 2016). Temporary wetlands also have a relevant role in some processes at a landscape or even a regional scale. For example, vernal pools in central Maine, United States, function as hotspots of leaf litter decomposition, denitrification and enzyme activity compared to adjacent upland forest sites (Capps et al., 2014).

In terms of their hydrology, temporary wetlands are known to be "nodes in hydrologic networks connecting landscapes in four dimensions—longitudinal, lateral, vertical, and through time" (Rains et al., 2016). Networks of temporary wetlands exist along a continuum of hydrologic connectivity from relative hydrologic isolation to predicted connectivity (Leibowitz et al., 2008; McLaughlin et al., 2014). Many temporary wetlands reduce peak floodwater flows, contributing to groundwater recharge or discharge (Euliss et al., 2004; Ganesan et al., 2016) and providing stream base flow. Temporary wetlands also provide lag, sink, and source (contribution) functions (as summarized by Rains et al., 2016) and "spill and fill" and "spill and merge" functions (Leibowitz et al., 2016) that have effects on the physical, chemical, and biological status of downstream waters.

Biodiversity

Temporary wetlands support a unique assemblage of biota adapted to living in temporary waters and hence contribute disproportionately to the biodiversity of both aquatic and semi-aquatic animals and plants (Williams, 2000; Herault and Thoen, 2009; Pinto-Cruz et al., 2009) by harboring rare and endemic taxa (Collinson et al. 1995; Marsh and Trenham, 2001; Calhoun et al., 2017; Mushet et al., 2019). In France, for example, vernal pools represent 0.05% of the natural habitats but hold around 35% of rare species and 5% of the protected plant species (Sajaloli and Limoges, 2001). The European Habitats Directive (European Directive 92/43/CEE) considers "Mediterranean temporary ponds" a priority habitat to conserve, but the Directive defines this wetland type strictly by the presence of particular plant species (European Commission 2003; Bagella et al. 2007). Moreover, obligate temporary species (i.e., some branchiopods) are examples of extremely rare species only known from selected ponds around the world (Alonso and García-de-Lomas, 2009; Cottarelli et al., 2010).

In addition to supporting rare and exclusive species, temporary wetlands also maintain metapopulation structure of many faunal groups, due to their importance as a foraging resource or breeding habitat (Griffiths, 1997; Wissinger, 1997). Many terrestrial mammals, amphibians, reptiles, and birds use the abundant resources in pools (i.e., egg masses, amphibian larvae and adults, invertebrates, algae and plants) to supplement their diets, especially following winter in temperate and boreal regions (Paton, 2005). Further, the absence in temporary wetlands of biotic groups not well adapted to drought allows the success of other biotic organisms susceptible to predation or competition (Wellborn et al., 1996). For example, the absence of fish (with few exceptions fish are not adapted to temporary waters; but see Pazin et al., 2006; Laufer et al., 2009; Lanés et al., 2014) in temporary wetlands increases the abundance and richness of invertebrate and amphibian specialists groups (Jeppesen et al., 2001). Fish predation may be a key factor in the structuring of communities (e.g., Brooks and Dodson, 1965; Brucet et al., 2010; Compte et al., 2011) and the flora and fauna of temporary wetlands in the absence of fish illustrates this well. Lastly, temporary wetlands also support biota that are terrestrial (Lott, 2010), or neither fully terrestrial nor fully aquatic (Jeffries et al., 2016). These additions to biodiversity are often overlooked in freshwater ecological studies (Mushet et al., 2019).

At landscape scales, temporary wetlands increase biodiversity through the addition of an aquatic feature (ephemeral to semi-permanent) in a terrestrial matrix that otherwise might include only permanent aquatic features. Temporary wetlands serve as aquatic stepping stones in an upland matrix and provide foraging and resting habitat for facultative species migrating to other resources. For example, in Europe, the agile frog (*Rana dalmatina*) can breed in different temporary ponds depending on the year (Guyetant, 1997), similarly the palmate newt (*Lissotriton helveticus*) can disperse across a network of temporary wetlands within a forest matrix (Isselin-Nondedeu et al., 2017). In the United States, the northern leopard frog (*Lithobates pipiens*) and bullfrog (*Lithobates catesbeianus*) overwinter in deep-water habitats, migrate to temporary wetlands for reproduction or feeding, and then return to deep-water habitats to hibernate (Mushet et al., 2013). Additionally, Mushet et al. (2019) found that over long temporal periods, the number of taxa accumulate and therefore contribute to biodiversity at a greater rate in wetlands with temporary ponds compared to those with more permanent water regimes.

Socioeconomic

Temporary wetlands provide valuable ecosystem services including wildlife habitat, nutrient flux to adjacent ecosystems, flood control, water filtration, and cultural services (e.g., Turner et al., 2008; Gascoigne et al., 2011; TSSC, 2012). For example, prairie potholes provide breeding habitat for over 50% of all North American duck populations, despite covering only a tiny portion of the area of their range (Baldassarre and Bolen, 2006), and support extensive recreational and educational opportunities. Gilgais are used by grazers to graze seasonally stock in areas that lack permanent water (Lachlan Riverine Working Group, 2016). Soaks associated with rocky outcrops, gnamma holes and gilgais were an important source of water for indigenous communities as they enabled people to forage seasonally over areas that lacked permanent water (see Fitzsimons and Michael, 2017). Given the connections between social, economic, and ecological importance of temporary wetlands, scientific advances documenting the range of ecological functions provided by these resources create opportunities for enhanced understanding and documentation of their socioeconomic importance (Bauer et al., 2017).

What Are the Current Threats and Management Challenges?

Inconsistent and Inadequate Regulatory Protections

The lack of rigor and consistency in regulatory protections for small aquatic resources is a global phenomenon (Acuña et al., 2017). For example, in Europe, Canada, and the United States many wetlands are exempt from regulation based on size or size of impact or are not regulated at all (see the European Water Framework Directive; Clean Water Act and Food, Conservation, and Energy Act of 2008 in the US; Mushet et al., 2014; Creed et al., 2017). In addition, wetland regulations typically target the wetland depression with little regard to adjacent terrestrial ecosystems or connectivity to other critical wetland resources (Cohen et al., 2016). Some small aquatic resources do receive enhanced protections, but such protections are afforded to a small subset of the resources (Bagella et al., 2007; Zacharias and Zamparas, 2010; Mushet et al., 2014; Levesque et al., 2019). The cumulative, landscape scale impacts of loss of small, temporary wetlands are not currently addressed in regulatory frameworks (Jansujwicz and Calhoun, 2017).

Climate Change

The tight relationship between hydrology and temporary wetlands makes them extremely vulnerable to changes in climate. By virtue of their small size (high watershed to surface area or volume ratio) and temporary hydroperiods, temporary wetlands are very responsive to changes in temperature and precipitation patterns (Fig. 2). The International Panel on Climate Change's predictions for the next 100 years suggest that temperature increases will be greatest in high latitudes, precipitation amounts and patterns will change, frequency of extreme storm events will increase, and sea levels will potentially rise 20–60 cm (Junk et al., 2013). Responses to climate change will vary across a gradient from arid to boreal regions, from individual wetlands and types, and across species (Calhoun et al., 2017). For example, temporary ponds and their biota in Mediterranean climates are more threatened by reduced precipitation, increased salinity, and extended droughts than temperate or boreal temporary wetlands (Boix et al., 2016). Precipitation events may become more extreme in some areas coupled with seasonal changes in distribution (Junk et al., 2013). Repeated droughts will increase decomposition rates of soil organic matter and change the composition of the vegetation that may contribute to carbon storage (Hervé et al., 2019). Extreme shifts in aquatic invertebrate biodiversity (Sim et al., 2013; Renton et al., 2015) and plant species composition (Ghosn et al., 2010; Bagella and Caria, 2013) may occur in all temporary systems as a result of changes in climate patterns (wetlands and waterways).

Changes in Land Use

Temporary wetlands are small, dynamic, and vulnerable to land-use changes. Moreover, temporary wetlands are threatened by ecosystem loss and degradation associated with land change and land management activities, pollution, resource extraction, and invasive species. For example, conversion and use of lands for urbanization, agriculture, and livestock (switching temporary wetlands to permanent pools; Beja and Alcazar, 2003; Euliss and Mushet, 2004); water extraction; other human-mediated impacts to biodiversity, including sedimentation (Grillas et al., 2004); and toxic pollution (Collins et al., 2014) can result in the modification or destruction of temporary wetlands. In every continent, invasive species are a major threat to wetland biodiversity (Brinson and Malvarez, 2002; Zedler, 2004). Although the period of time without water impedes the colonization by exotic fishes, many exotic and specially adapted species have invaded temporary waters, including plants (Collinge et al., 2011; TSSC, 2012; Brundu, 2015), crayfishes (Carreira et al., 2014; Rodríguez-Pérez et al., 2014), and amphibians (Escoriza et al., 2014; Meilink et al., 2015). These invaders have contributed to the loss of species, wetland functions, food web dynamics, and habitat structure.

Management Challenges

Ecological

Temporary wetlands require management at both local and landscape scales; they are active biological, physicochemical, and ecological nodes in a terrestrial matrix (Grillas et al., 2004; Amis et al., 2009; Mushet et al., 2014; Golden et al., 2019). Since temporary wetlands are defined by hydroperiod, they are extremely susceptible to changes in land-use patterns and activities beyond the wetland footprint that alter hydrologic patterns. Because most temporary wetlands have high perimeter to surface area ratios and relative low volume with limited inlet and outlets, if present at all, they are also quite sensitive to alteration in chemistry from sediments and pollutants. In addition, many temporary wetlands support wildlife with biphasic or complex life histories involving annual migrations of hundreds of meters, making the adjacent terrestrial habitat an integral part of conserving their functions (Semlitsch, 2002; Bird and Day, 2014; Groff et al., 2017). Direct losses or fragmentation of wetlands, particularly ephemeral ponds, decreases wetland density increasing travel distances for biota, particularly those organized in metapopulations, using multiple aquatic resources (Gibbs, 1993).

Conservation of temporary wetlands ecosystems is made difficult by trends in conservation priorities, funding, and research that discount these resources (Martín-López et al., 2011) and therefore undercut scientific understanding of multi-scale processes. One major challenge is then to manage, conserve, or restore by integrating spatial scales from wetland to landscape, taking into account all fluxes of energy, materials and organisms. Clearly, one will not be able to manage for all things, but being aware of the implications of management is important at any scale.

Social

Limited public awareness of, incomplete understanding of the ecosystem services provided by, and cost:benefit issues associated with the conservation of temporary wetlands can complicate their management. For many temporary wetlands, public understanding of their functions is limited, diminishing support for public conservation actions (Mushet et al., 2014; Marton et al., 2015; Cohen et al., 2016). Two exceptions provide inspiration for addressing the challenge of limited public awareness. The importance of temporary wetlands in supporting breeding waterfowl in the Prairie Pothole Region is widely recognized and led to the region becoming known as the "duck factory of North America" (Lynch, 1984; Batt et al., 1989). Educational outreach has also helped to reverse some forestry practices detrimental to temporary ponds in the region of Chinon in France where it has been estimated that 90% of temporary wetlands were destroyed after intensive tree plantation and drainage (Couderc, 1979; Isselin-Nondedeu et al., 2013). Less visible ecosystem functions, however, such as biogeochemical and stream base flow support, are often not well-documented and are easily underappreciated or devalued (Millennium Ecosystem Assessment, 2005). Ecosystem services of temporary wetlands will have to be better quantified and explained to change perceptions of value and support for different management structures. The spatial mismatch between conservation benefits and costs can also challenge management of temporary wetlands. While the social importance of temporary wetlands can be quite significant (because they are the summation of many values held by society), temporary wetlands may offer individual landowners only limited private value relative to competing uses of lands. Management approaches that recognize the spatial distribution of benefits and costs and full extent of conservation costs are more likely to navigate these challenges successfully (Shogren et al., 2003; Bauer et al., 2010, 2017; Jansujwicz et al., 2013; Sunding and Terhorst, 2014; Levesque et al., 2016).

Public valuing of temporary wetlands could lead to enhanced inventories. To effectively manage temporary wetlands, it is essential to have a spatially explicit inventory and assessment of their ecological status and the context of the terrestrial matrix (Van Meter et al., 2008; Van den Broeck et al., 2015). Still, detailed wetland inventories are lacking in large sections of the world (e.g., China, South America, Russia), and small wetlands are often disregarded or not captured in places where inventories are conducted (Robertson and Fitzsimons, 2004; Junk et al., 2013). In addition, information may be available but poorly accessible and dispersed across agencies or private entities. If wetlands are mapped remotely, the ability to identify these features will vary greatly depending on the nature of the matrix. For example, in forested landscapes containing vernal pools in midwestern and northeastern North America, remote detection is problematic, often missing as much as 30% of pools (Tiner et al., 2015; Dibello et al., 2016). Even in open areas, remote detection of small wetland features can be limited by atmospheric conditions or spatial resolution of the sensor being used (Rover and Mushet, 2015). However, as technologies continue to improve (e.g., Wu and Lane, 2017), the ability to remotely detect and map small wetland features will continue to improve, especially with 3-D digital technology and high resolution LiDAR and Synthetic-Aperture Radar (SAR) approaches (Tiner et al., 2015; Wu and Lane, 2017).

Approaches for Conserving Temporary Wetlands

The most suitable approaches for conserving temporary wetlands include regulations or other forms of protection; sustainable management; collaborative conservation; and restoration and creation. Regulations or other forms of protection range from restrictive local protections conserving temporary wetlands and adjacent habitat to broader national regulations (e.g., the listing of the "Seasonal Herbaceous Wetlands [Freshwater] of the Temperate Lowland Plains" ecological community as critically endangered under national threatened species/communities legislation in Australia). Top-down regulation (at any government level) has the advantage of setting clear rules but may suffer from lack of enforcement or "buy in" from the stakeholders being regulated. Protection may also result from crisis management of increasing threatened or rare temporary wetlands. For example, in southeastern Australia, ephemeral wetlands such as gilgais typically occur on fertile country which was privatized and suffered from conversion to more intensive agricultural activities. Efforts to increase the representativeness of Australia's reserve system has seen the acquisition of a number of significant properties containing temporary wetlands (e.g., Fitzsimons and Ashe, 2003; Fitzsimons et al., 2004).

Small natural features, including temporary wetlands, are arguably best managed using the meso-filter approach (Hunter, 2005), where features that may be small ecosystems in their own right or ecological elements within larger ecosystems can, by nature of their small size, open the door to sustainable management. Management approaches (including landowner incentives) will range from practices specific to land uses adjacent to temporary wetlands to landscape-scale approaches that recognize the functions of temporary wetlands as wetland complexes embedded in, and likely integral to, other ecosystems. For example, in arid and semi-arid Australian rangelands, gilgai conservation was considered a key feature in market-based incentives for landholders to better manage grazing (Smyth et al., 2007). In southeastern Australia, market-based auctions for conservation actions have been in place for the past decade and would prioritize ephemeral wetland communities due to their conservation status based on past loss and ongoing threats. Integration of vernal pools as a component of forest biodiversity is a way to manage sustainably both terrestrial and aquatic habitats. In many national forests in France and commercial forests in the northeastern United States, the application of best management procedures includes reducing disturbance immediately adjacent to pools by implementing management zones around the pools and implementing standards for maintaining uneven aged forest stands (Calhoun and deMaynadier, 2004; Guittet et al., 2015).

Similarly, a market-based approach has been developed in New England, United States, to manage vernal pools in developing landscapes. A creative, voluntary, hybrid approach—a community based collaborative effort that draws from both top-down (a regulatory "stick" or incentive) and bottom-up regulatory restrictions—has generated great interest as a new conservation tool (Freeman et al., 2012; Calhoun et al., 2014b; Levesque et al., 2016, 2019; McGreavy et al. 2016). In this program, impacts to pools in developing areas generate fees from developers to conserve vernal pool landscapes in rural areas in the same town (Special Area Management Plan for Vernal Pools in US Army Corps of Engineers Region 1; Levesque et al., 2016, 2019).

Collaborative voluntary approaches may evolve without the regulatory "stick." For example, in Australia, collaborative landscape-scale arrangements such as Conservation Management Networks (biophysical networks of remnant vegetation sites across a variety of tenures and a social network of managers, owners, and interested people) have also been applied in fragmented landscapes containing temporary wetlands (Edwards and Fox, 2013; Fitzsimons et al., 2013). These arrangements seek to (a) increase the protection status of sites; (b) maintain, enhance and re-establish remnants across private and public land; (c) bring together owners and managers of vegetation remnants; (d) connect and buffer remnant patches; and (e) develop consistent and complementary management across sites, and are across tenures.

Sustainable management in the face of climate change necessitates approaches that, as Beier et al. (2015) recommend, conserve "nature's stage." This approach moves conservation away from focusing on dynamic targets such as community types, e.g., spruce-fir forests or wood frog breeding pools, to capturing the physical features that support the array of defining characteristics of any given ecosystem target. For temporary wetlands, this would mean conserving an array of hydrogeomorphic settings (ones that support short to long hydroperiods in different physical settings) to allow a range of biogeochemical and water quality functions as well as support of diverse biota (Marton et al., 2015); this approach increases the chances that species and processes can evolve with changes in climate. In addition, the importance of allowing for gene flow among diverse temporary pool communities is highlighted by Rice and Emery (2003) and others who advocate for maintaining or restoring microevolutionary processes to meet the challenges of a shifting climate.

Restoration or creation of temporary wetlands (Fig. 4) may result from legal restrictions on impacts that require mitigation for wetland losses or from voluntary efforts to ameliorate losses. An inability to recreate hydrology is often the cause of a failure in restoring or creating temporary wetlands, particularly for pool-breeding amphibians and invertebrates (Petranka et al., 2007; Calhoun et al., 2014a; Drayer and Richter, 2016). In the North American Prairie Pothole Region, efforts to restore plant communities of temporary wetlands typically result in communities of lower floristic quality compared to plant communities of undisturbed wetlands (Mushet et al., 2001, Salaria et al., 2019), but successes in plant restoration have been reported in other regions of the United States (Ferren and Hubbard, 1998). In gilgai depressions in southeastern Australia, increased floristic biodiversity occurred with removal of grazing, while gilgai microrelief homogenized by cultivation showed some recovery after release from cultivation (Nolan et al. 2018). In addition, landscape setting and condition and location with respect to other aquatic resources is important to wetland functions. It is challenging to recreate natural wetland functions in off-site areas that might not be conducive to natural wetland conditions.

In situations where wetland losses are high, wetland restoration or creation may be a good option. For example, efforts to restore vernal pools in France and Spain have attempted to create short hydroperiods by digging shallow pools that are very dependent on precipitation. Initial results concerning abiotic functions and amphibian colonization are promising (Ruhí et al., 2012; Isselin-Nondedeu et al., 2013). However, even after relatively long periods post restoration, communities and ecological functions in many temporary wetlands are often not entirely restored (Ruhí et al., 2009; Matthews and Spyreas, 2010; Moreno-Mateos et al., 2012; Ruhí et al., 2016, Salaria et al., 2019). Creating temporary wetlands where they previously did not exist is an even greater challenge.

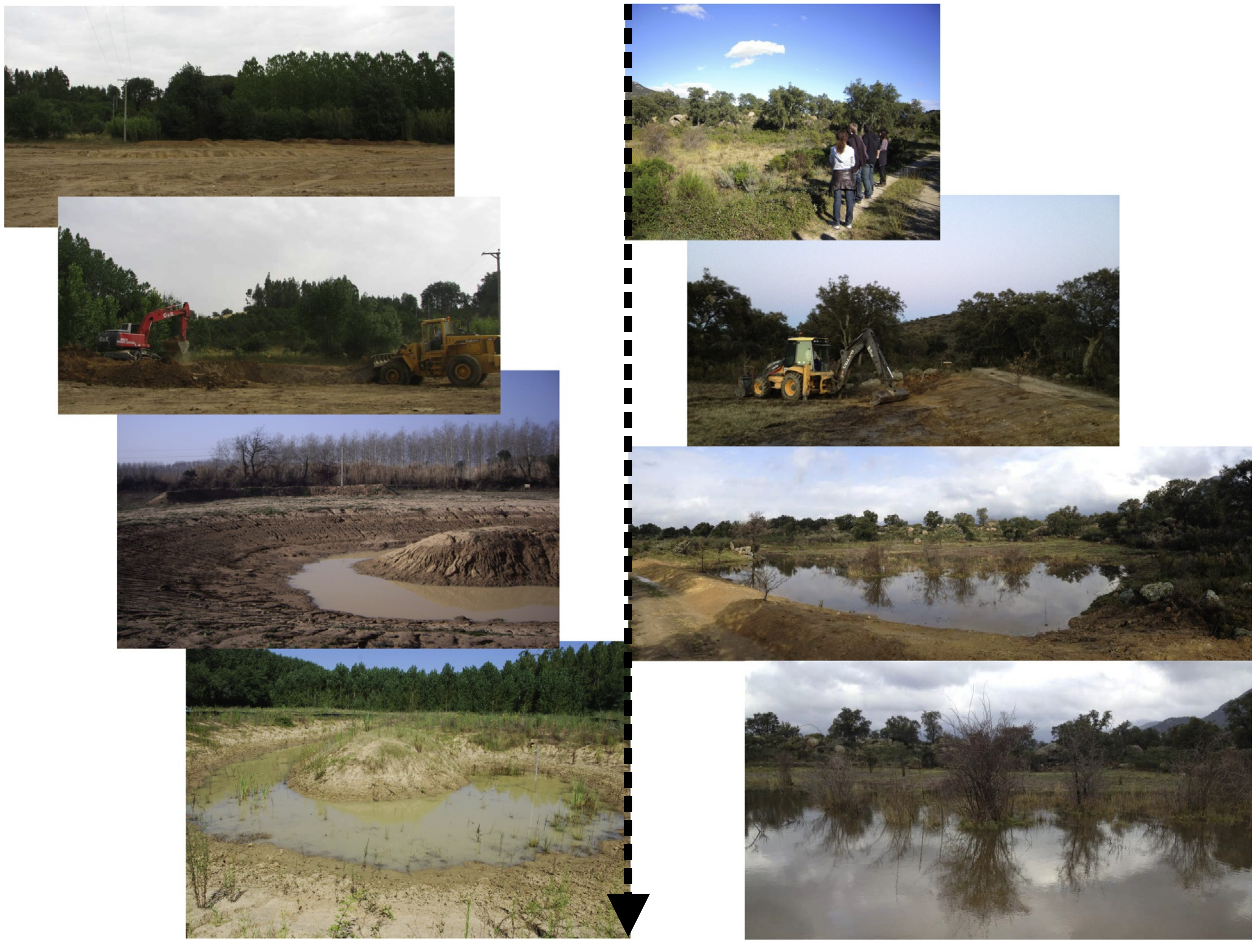


Fig. 4 Examples of temporary wetland restoration projects developed in NE of Iberian Peninsula. Left side, creation of temporary ponds to reinforce amphibian populations in Esplet, La Selva, Spain (photos: A. Ruhí). Right side, restoration of the "Bassa del Pla dels Rosers" in Albera, Alt Empordà, Spain (photos: M. Pascual and J. Montaner).

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