Characterization and Global Distribution of Vernal Pools

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Abstract. We define vernal pools as precipitation-filled seasonal wetlands inundated during periods when temperature is sufficient for plant growth, followed by a brief waterlogged-terrestrial stage and culminating in extreme desiccating soil conditions of extended duration. These factors have played a significant selective role in shaping the vernal pool flora and fauna. Inundation during the growing season largely eliminates establishment of upland species in the pool basins and the terrestrial period is sufficiently desiccating to prevent establishment of many typical wetland taxa. Pool filling is predominantly from precipitation and drainage is from a relatively small watershed, consequently nutrient input is largely autogenous. Vernal pools tend towards oligotrophic and are poorly buffered with dramatic diel changes in CO_2, O_2, and pH. These factors have played a role in selection of CAM photosynthesis in *Isoëtes* and *Crassula*, and may further contribute to elimination of many other typical wetland plants. The flora comprises two elements: cosmopolitan aquatic taxa and vernal pool specialists. The former are species in genera found worldwide in aquatic habitats, whereas specialists are species from terrestrial genera in western North America. While the fauna includes vernal pool endemics, most all species are in globally widespread aquatic genera. California vernal pools comprise a diverse array of seasonally aquatic habitats. Although variable in their origin, size, shape, type of duripan, depth, duration of inundation and species composition, three factors (duration, timing, and source of inundation) are common across all systems generally classified as Californian vernal pools. Outside of California, vernal pools are present in other Mediterranean climate regions, being best developed in Chile and Western Australia. Vernal pools are also found in non-Mediterranean climates, for example on the well-studied "granite outcrops" of the southeastern U.S., where shallow basins fill during the winter and, despite summer-rains, high temperatures and shallow substrates result in desiccating summer conditions. Other seasonal wetlands such as desert playas, Great Plains buffalo wallows and prairie playas or potholes have sufficient differences to be excluded by our definition of a vernal pool.

Introduction

Are California vernal pools unique? This question has been addressed several times in the literature often with conflicting conclusions. In the opening paper to a 1976 vernal pool proceedings volume Stebbins (1976) stated "California's vernal pools are unique habitats," whereas in a later proceedings Thorne (1984) concluded that vernal pools "are widely distributed about the various continents of the world, generally in areas enjoying a Mediterranean type of climate." Although subsequent investigators have continued the debate as to whether or not this habitat is uniquely Californian, most seem to believe there is a close association between vernal pools and the Mediterranean climate (Zedler 1987; Ferren and Fiedler, 1993; Keeler-Wolf et al., 1995). However, this Californian perspective is not universal, as the term "vernal pools" is used to describe habitats in

other climatic regions (e.g., the southeastern U.S., see Radford et al., 1964). Also, vernal pool-like habitats are included under a variety of terms throughout the world, including "ephemeral wetlands," "vernal marshes," "buffalo wallows" "seasonal pools," "vleis," and "temporary waters," and this is by no means an exhaustive list.

Here we approach the task of characterizing the vernal pool habitat, and these questions of uniqueness and climatic association, as follows. We first define the characteristics that tie together the range of habitats commonly considered California vernal pools and then examine the biotic features that distinguish them from other wetland habitats. We then contrast the vegetation characteristics of these vernal pools with similar seasonal wetland systems in other parts of the world.

Defining The Vernal Pool Habitat

In the most general terms, vernal pools are seasonal wetlands that form in shallow basins and alternate on an annual basis between a stage of standing water and extreme drying conditions. In greater detail we can recognize four stages in an annual vernal pool cycle that include (i) a wetting phase, (ii) an aquatic or inundation phase, (iii) a waterlogged-terrestrial phase, and (iv) the drought phase (as modified from Zedler, 1987). Under the Cowardin (Cowardin et al., 1979) system, vernal pools are classified as seasonally flooded emergent wetlands of the palustrine system (Ferren and Fiedler, 1993). There are of course other classification systems (e.g., Scott and Jones, 1995; Semeniuk and Semeniuk, 1995), although these systems do not adequately incorporate what some authors consider to be an additional distinguishing feature of vernal pools, namely that they are largely rain-fed (Zedler, 1987; Ferren and Fiedler, 1993). We contend that three elements are needed to define the vernal pool habitat:

(1) Source of water.
(2) Duration of the inundation and waterlogged phases.
(3) Timing of these phases.

Thus, we define vernal pools as "*precipitation-filled seasonal wetlands inundated during periods when temperature is sufficient for plant growth, followed by a brief waterlogged-terrestrial stage and culminating in extreme desiccating soil conditions of extended duration.*" While the Mediterranean climate of mild wet winters and hot dry summers is conducive to the formation of vernal pools, climate is neither explicitly part of our definition, nor, as will be illustrated later, is it a necessary component. Each of these elements – source, duration, and timing of inundation – have played an important selective role in the evolution of the vernal pool biota, both in California and in other regions.

Source of Inundation

Vernal pools fill from precipitation during periods when the rate of water input exceeds the rate of water loss, primarily from evapotranspiration (Zedler, 1987). This requires depressions in soils overlying an impervious substrate, which inhibits downward percolation, resulting in a perched water table. Depending upon topography, and duration and intensity of precipitation, some pools may receive surface and subsurface flow of water (Hanes et al., 1990; Hanes and Stromberg, 1998). A factor that separates vernal pools from other seasonal, as well as permanent, wetlands is the lack of water input by long-distance drainage. Therefore, unlike formal classification systems such as the Cowardin Scheme and modifications of it (Ferren and Fiedler, 1993), we do not include stream-fed seasonal wetlands in our definition of vernal pools. The primary reason is that much of the character of seasonal wetlands changes with allochtonomous

nutrient addition resulting from water flowing into or through a pool basin (Wetzel, 1975). Another factor is that temporary wetlands in drainages are subject to periodic scouring in years of high flow, which is not conducive to the persistence of a system strongly dependent upon buried propagules and the development of mature soils with clay subsoils.

One consequence of being primarily rain-fed is that vernal pools tend to have low nutrient levels and water chemistry is generally more similar to that of oligotrophic lacustrine habitats, which are typically found at higher elevations and latitudes (Keeley, 1991). Water conductivity is often proportional to concentrations of the major ions (Wetzel, 1975) and is at the low end of the spectrum for aquatic systems. For example, an oligotrophic high Sierran lake would likely have a specific conductance $_{(@ 25oC)} < 25$ μmhos cm^{-1} and a low elevation eutrophic lake might be > 500 μmhos cm^{-1}; vernal pools in southern California are typically 40-70 μmhos cm^{-1}, although this increases sharply as the pools dry and ions are concentrated (e.g., Keeley and Morton, 1982; Keeley, 1983; Keeley et al., 1983). However, soil type may alter this pattern and some alkaline pools (e.g., Stone et al., 1988; Keeler-Wolf et al., 1995) are likely to have substantially greater salinity.

A consequence of low nutrients, is that vernal pool waters are unbuffered and undergo extreme diurnal changes in pH and levels of dissolved carbon dioxide as well as oxygen (Figure 1). Due to the very high surface to volume ratio of these shallow basins, most experience extreme diel changes in temperature as well. Thus, early in the day they may present relatively luxuriant growing conditions, but as light increases, photosynthesis is inhibited by carbon dioxide limitation, and potentially oxygen inhibition via photorespiration (Keeley and Busch, 1984). In these unbuffered waters, pH is largely controlled by the carbon dioxide-bicarbonate system and thus when waters experience photosynthetically-driven depletion of CO_2, the pH may rise 2-3 pH units over a matter of hours (Figure 1). One practical consequence of this dynamic is that regional pH comparisons are not possible because, other than the studies cited above, reports of water pH have not included time of sampling, let alone a diurnal time course.

This pool chemistry dynamic is not typical of all wetland environments (Keeley, 1991) and represents an important evolutionary force that has selected for unexpected photosynthetic pathways. For example, vernal pool species such as *Isoëtes howellii* and *Crassula aquatica* [nomenclature for California plants is according to Hickman, 1993] utilize CAM photosynthesis normally associated with desert succulents, and the resulting nighttime carbon fixation contributes substantially to the total carbon budget (Keeley and Sandquist, 1991). Also, vernal pool endemics in the Orcuttieae Tribe of grasses have C_4 photosynthesis, a pathway more typical of subtropical savanna
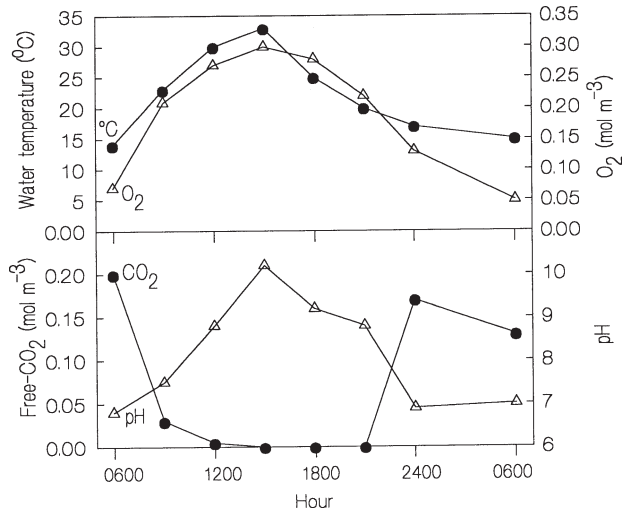
FIGURE 1. Diel changes in physical and chemical charcteristics for a southern California vernal pool (data from Keeley 1983, and unpublished).

grasses, which is considered to be adaptive under these pool conditions (Keeley, 1998a).

In summary, the bulk of the water causing inundation of vernal pools enters via precipitation and very local runoff and generally leaves largely by evapotranspiration, with varying levels of seepage. Soil nutrients are derived locally. These factors contribute to an aquatic milieu that is potentially carbon-limited and may be a contributing factor in the absence of some typical aquatic taxa (e.g., Table 1).

Duration and Timing of Phases

In California, inundation of pool basins during the winter/spring growing season is sufficient to prevent typical upland plants from occupying these seasonal wetlands. Equally important, vernal pools dry during the summer and soils are sufficiently desiccated that many typical aquatic and wetland species are prevented from establishing. Examples of upland and wetland plant genera that are widely distributed in California, but effectively eliminated from the vernal pool habitat, are shown in Table 1.

Selective Role of Inundation. The impact of the length of the inundation phase on the floristic composition of vernal pools is visualized by plotting species replacement along an elevational gradient of <100 cm, extending from the edge of pools to the center (e.g., Lin, 1970; Kopecko and Lathrop, 1975; Holland and Jain, 1984; Zedler, 1987; Bauder, 1987a) and such a gradient correlates with inundation period (Figure 2). At the highest microsites, those experiencing little or no inundation, are annual grasses and forbs (Table 1) that are usually distributed outside the pool basins and comprise the surrounding grass-

TABLE 1. Native and introduced California vascular plant genera typical of upland sites in grasslands and freshwater wetland habitats in close juxtaposition with vernal pools (from Zedler, 1987; Mason, 1957). This is not an exhaustive list but rather represents examples of genera that are common in adjacent or nearby habitats but are excluded from the vernal pool habitat. Nomenclature used in tables and text follows Hickman (1993), or source cited. A = annual, P = perennial.

Upland Taxa	Wetland Taxa
Anthophyta – Dicots	Anthophyta – Dicots
Erodium (A)	*Anemopsis* (P)
Filago (A)	*Ceratophyllum* (P)
Hemizonia (A)	*Ludwigia* (P)
Medicago (A)	*Myriophyllum* (P)
Microseris (A)	*Polygonum* (A,P)
Malvastrum (A)	
	Anthophyta – Monocots
Anthophyta – Monocots	*Alisma* (P)
Agrostis (A,P)	*Echinodorus* (A)
Avena (A)	*Elodea* (P)
Bromus (A)	*Glyceria* (P)
Lolium (A)	*Potamogeton* (A,P)
Vulpia (A)	*Sagittaria* (P)
	Sparganium (P)
	Typha (P)

land flora. Lower in the pool basin are plant taxa restricted to the vernal pool habitat (Table 2). Thus, vernal pool plants exploit habitats that competitors, dominant in adjacent grasslands, are excluded from due to their lack of tolerance to inundation during the growing season (Zedler, 1987; Bauder, 1987a). Additional evidence that grassland species are excluded from pool basins due to their lack of inundation tolerance is their ability to colonize pool basins in low rainfall years (Zedler, 1984; 1987; Bauder, 1987a; 1987b).

Selective Role of Drying. California has a large number of aquatic/wetland species (Mason, 1957) that do not occur in vernal pools (Table 1). We hypothesize that this is due to their inability to tolerate the soil desiccation and heat (e.g., soils > 70°C) associated with summer droughts. Indeed, summer surface soil moisture conditions are indistinguishable from those of adjacent uplands. The timing of pool dry-down, in mid- to late spring, is also important in the exclusion of upland plant species. It occurs when air temperatures are rising rapidly and this transition period, between inundation and drought, is too brief for establishment of typical "emergent" wetland plants (Table 1).
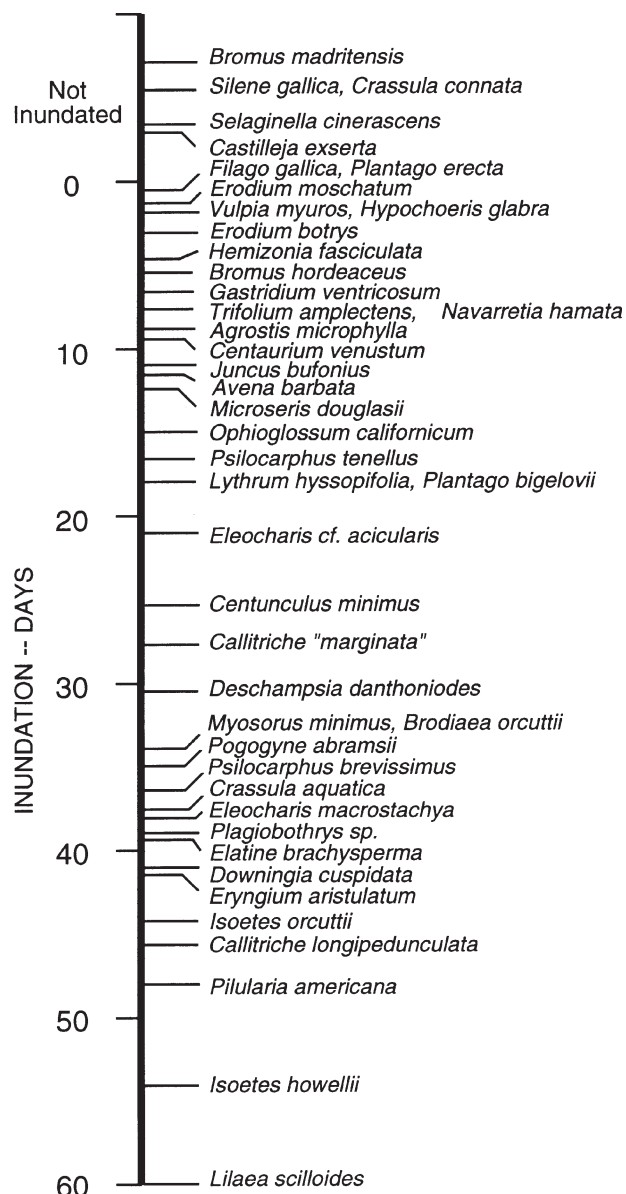
FIGURE 2. Average water duration class for common vernal pool species for a Kearney Mesa, southern California (from Zedler 1987).

TABLE 2. California vernal pool plant genera with one or more species in vernal pools (compiled from sources cited in text). A = annual, P = perennial..

Cosmopolitan Aquatics	Vernal Pool Specialists
Lycophyta/Cterophyta	Anthophyta – Dicots
Isoetes (P)	*Blennosperma* (A)
Marsilea (P)	*Chamaesyce* (A)
Pilularia (P)	*Downingia* (A)
	Eryngium (P)
Anthophyta – Dicots	*Gratiola* (A)
Callitriche (A)	*Lasthenia* (A)
Crassula (A)	*Legenere* (A)
Elatine (A)	*Limnanthes* (A)
Myosurus (A)	*Navarretia* (A)
Ranunculus (A,P)	*Pogogyne* (A)
	Plagiobothrys (A)
Anthophyta – Monocots	*Psilocarphus* (A)
Eleocharis (P)	
Lilaea (A)	Anthophyta – Monocots
	Neostapfia (A)
	Orcuttia (A)
	Tuctoria (A)

and thorough surveys of the site in June of those years failed to uncover any vernal pool plant remains (Keeley, unpubl. data). Instead, pool basins were dominated with the dried remains of typical upland annuals (Table 1).

In summary, California vernal pools are dominated by a flora comprising species that represent a specialized aquatic lifeform, one adapted to periods of inundation alternating with annual desiccation.

CHARACTERIZING CALIFORNIA VERNAL POOLS

As discussed below vernal pools are not restricted to Mediterranean climates, but in California climate plays a key role in generating standing water during the spring growing season and desiccation during the summer drought. Another important factor contributing to the widespread presence of vernal pools is topography. At the landscape level in California, three of the primary geomorphological origins of pools are: (i) coastal terraces in southern California, (ii) alluvial terraces in the Central Valley and (iii) eroded lava flows in several parts of the state (Holland, 1978; Keeler-Wolf et al., 1995). At a local scale, pools can only form in closed and shallow depressions on relatively level terrain. However, pools form in depressions originating from a diverse set of biotic and abiotic conditions (Norwick, 1991). Basin shape and size play important roles in determining the extent of subsurface water-flow into the pools. Differ-

Not only has the vernal pool flora evolved an annual summer dormancy cycle but it is also capable of remaining dormant for several years in succession (e.g., Crampton, 1959; Griggs and Jain, 1983; Holland, 1987; Stone et al., 1988). This is best illustrated by example. In a wet year the Stanislaus County Hickman Pools typically cover hundreds of hectares and in September of the very wet 1993, one of the smaller pools (Pool A, in Stone et al., 1988) still covered several hectares. The moist margins supported dense populations of the vernal pool endemic grasses *Neostapfia colusana* and *Orcuttia pilosa*, and many of them were still green (Keeley, unpubl. data). However, during the three-year drought preceding 1993, this pool did not fill

ences in topography may affect the duration of different phases. For example, large basins with substantial sub-surface flow may prolong the duration of the waterlogged phase and shorten the duration of the desiccation phase. Soils are typically heavily weathered with topsoils high in clay and range from acidic to alkaline. An additional geomorphological feature necessary for pool formation is an impervious duripan layer beneath the depression, which inhibits downward percolation of water. This may be generated by cemented pedogenic hardpans, rock, volcanic deposits or clay lenses (Zedler, 1987). Potentially, pools could form from rises in the water-table, but available data suggest that almost all pools form because of very locally perched water, with the surface of the water table declining away from the pools (Napolitano and Hecht, 1991).

Vernal pools form a rich array of different types of ecosystems and vegetation associations and these have been reviewed and classified (Holland, 1986; Keeler-Wolf et al., 1995; Sawyer and Keeler-Wolf, 1995). Soil type and topography are implicated as primary factors determining the vegetation association (Holland and Dains, 1990). Soil type will affect water chemistry and will alter community composition; e.g., alkaline-saline pools typically have very different floras than acidic pools. Duration of the different phases of the pool cycle may also affect community composition. For example, basin size and shape may act to enhance subsurface water flow, which in turn could extend phase (iii) the terrestrial waterlogged phase. Such conditions might favor establishment of perennial wetland species, e.g., *Eleocharis macrostachya*, producing a habitat more aptly described as a vernal marsh than a vernal pool. Basin depth is likewise an important factor driving community composition. Deeper basins will retain water longer and favor different assemblages (Figure 2). Annual variation in weather patterns will also affect the duration of different phases and this has marked impacts on community composition. It is not uncommon that within the same pool different species will dominate in different years.

The Flora

Vernal pool species germinate or sprout from vegetative structures during either the wetting phase (i) or the inundation phase (ii). A number of species are known to initiate germination during the wetting phase (Zedler, 1987; Bauder, 1987a) whereas others appear to require inundation (Keeley, 1988). The timing and duration of these phases may play key roles in determining community composition (Bliss and Zedler, 1998). During the inundation phase, many species produce foliage that is distinct from the foliage produced upon exposure to the aerial environment. There is a remarkable degree of convergence in the isoetid growth form, characterized by rosettes of terete leaves with extensive lacunal airspace. It is present in distantly related species such as *Isoëtes orcuttii*, *Orcuttia californica*, *Lilaea scilloides*, *Navarretia myersii*, *Eryngium aristulatum*, and

Plagiobothrys undulatus. This growth form enhances carbon assimilation (Keeley, 1990; 1991; 1998c) and in some genera, e.g., the latter three listed above, it is not produced by closely related terrestrial species (Spencer and Rieseberg, 1998; Keeley, unpubl. data). Also, during the inundation phase some taxa, e.g., *Marsilea vestita*, *Alopecuris howellii*, *Callictriche* spp., and *Orcuttia* spp., produce floating leaves that are laminate and structurally distinct from submerged foliage (Keeley, 1990).

As the water level drops and the pools enter phase (iii) the soils are moist to waterlogged and plants persist in a terrestrial environment. Most all species undergo a metamorphosis and cylindrical foliage is replaced with laminate foliage. For the majority of species, flowering is initiated during this phase.

The upper elevational borders of pools often comprise a mixture of typical upland species (e.g., species of *Bromus* and *Erodium*) and more narrowly restricted pool species (Figure 2). In the California flora there are more than 100 vascular plant species that are either restricted to vernal pools or are more commonly associated with vernal pools than with other habitats, although a typical pool will usually have only 15-25 species (Holland and Jain, 1977; 1984; Zedler, 1987; Stone, 1990). The desiccating summer soil conditions favor annuals over perennials and even many of the perennial species suffer extensive mortality and function more like annuals (Zedler et al., 1990). An exceptionally large percentage of the vernal pool flora is composed of annuals (80%), which is significantly greater than for the flora of other communities in the California Floristic Province (Zedler, 1990).

An important characteristic of the vernal pool flora is that it comprises two elements: widespread cosmopolitan aquatic taxa and specialized Californian endemics (Table 2). Cosmopolitan taxa are widespread aquatics that are not restricted to Californian vernal pools, e.g., *Callitriche heterophylla*, *Crassula aquatica*, *Elatine chilensis*, *Eleocharis acicularis*, *Isoëtes howellii*, *Lilaea scilloides*, *Marsilea vestita*, *Myosurus minimus*, and *Ranunculus aquatilis*. Some of these species and all of these genera are found worldwide in a diversity of aquatic habitats. The endemic element includes species that are endemic to California vernal pools and most such species are in genera not associated with aquatic habitats (Table 2). There is some evidence these vernal pool endemics are derived from terrestrial ancestors and thus we describe this element as the vernal pool specialists. Several taxonomic works have noted the specialization of vernal pool species, relative to upland congeners, e.g., *Navarretia* (Crampton, 1954), *Blennosperma* and *Lasthenia* (Orndúff, 1963). Spencer and Rieseberg (1998) provide a rather detailed illustration of this pattern in *Navarretia*. Another example of evolutionary specialization to the vernal pool habitat is the Orcuttieae tribe of grasses, which comprise just three genera, the monotypic *Neostapfia*, three *Tuctoria* and five *Orcuttia* species (Reeder, 1982). All are C_4 annuals endemic to

5

vernal pools, seven of which are endemic to California and cladistic analysis supports the conclusion that these are derived from terrestrial ancestors (Keeley, 1998a).

The Fauna

In California, the concept of a vernal pool as a unique habitat developed around the endemic-rich flora (Zedler, 1987). There has been, however, a long-standing appreciation of the unique vernal pool fauna, which includes a number of endemic species (Keeler-Wolf et al., 1995). At the higher taxonomic levels (genus and above), this fauna is essentially a subset of a worldwide group of invertebrates adapted to shallow, temporary fresh waters with a very long history of adaptation to these habitats (Belk, 1984; Williams, 1987). The quintessential group fitting this description is that of the "larger branchiopods," crustaceans (following Belk, 1996) in the class Branchiopoda and the orders Anostraca (fairy shrimp, brine shrimp), Conchostraca (clam shrimp), and Notostraca (tadpole shrimp). Families, genera, and some species within these groups are cosmopolitan, and the large majority of taxa occur only in ephemeral waters. The parallels with the life histories of vernal pool annual plants are striking. For example, all three orders are capable of surviving through prolonged hot, dry, periods; often by means of embryos in arrested development ("cysts"). For most species, the first stage larvae emerge soon after pool filling. Although there are exceptions, generally species of larger branchiopods are absent from habitats with the abundance of predators expected in more permanent waters (e.g., dragon fly larvae, notonectids, dytiscid beetles, fish), and this includes the later stages of temporary habitats when the abundance of predators is usually at a maximum (e.g., Dubbs, 1987; Lake et al., 1989).

Ostracods (Class: Ostracoda) are another crustacean group characteristic of temporary freshwater habitats throughout the world, though a majority of species are found in a wide range of other habitats, including the oceans and estuaries. The temporary water taxa of ostracods share the general life history traits of the branchiopods, with early emergence (Dubbs, 1987) and a remarkable ability to survive prolonged drought by the production of drought resistant eggs (Delorme, 1991).

The distribution of many genera of these temporary pool specialists is vast. For example, *Branchinecta*, an anostracan genus abundant in California pools, is found on every continent but Australia; *Streptocephalus* and *Linderiella* are found throughout the northern hemisphere and in Africa (Williams, 1987). The notostracan genera *Lepidurus* and *Triops* are both found on every continent except Antarctica (Belk, 1996). Other genera are more restricted but still widespread – 10 of 23 anostracan genera reported by Belk occur on only a single continent (Belk cited in Williams, 1987).

These large distributions are consistent with a long history. The first known fossil Anostracan is from the upper Cambrian (Belk, 1996). Lower Cambrian ostracods are said to be the oldest known microfauna (Delorme, 1991), and they were well diversified by the Ordivician, when plants were only beginning to invade the land (Doyle, 1996). Study of fossil and extant conchostracans has established the presence of the group in the Paleozoic. It seems likely that branchiopods and ostracods and perhaps all the other groups were among the many organismal types that emerged in the "Cambrian revolution."

The continuity in ecological specialization is illustrated by Tasch's study of fossil conchostracans which shows that during the Paleozoic and Mesozoic their primary if not exclusive habitat was fresh waters, and that many genera were widely distributed across Gondwanaland (Tasch, 1987). He notes that endemism was primarily at the specific level. The continents have drifted, but overall pattern of regional specialization of widespread higher taxa of ancient lineage describes many of the extant vernal pool crustacean groups.

We are only now beginning to appreciate the biodiversity of the vernal pool invertebrate fauna. Taxonomic difficulties have obscured the degree of species diversity and patterns of endemism in the vernal pool fauna. Recent studies have uncovered a previously unknown degree of speciation and endemism within the crustacean groups. This is primarily at the specific level, with many widespread genera (e.g., *Branchinecta* [Anostraca], *Candona* [Ostracoda], and *Alona* [Cladocera]) having multiple local or regional species that seem to be restricted to ephemeral waters (Eng et al., 1990; Fugate, 1993; King et al., 1996). The argument can therefore be made that the crustacean fauna ties together world-wide ephemeral habitats better than plants do, both spatially—because many specialist taxa are very widespread geographically—and temporally because the assemblages of extant pools are probably very similar in form and function to those as far back as the Mesozoic.

The patterns of distribution and endemism in the larger branchipods and ostracods may be compared to that of the cosmopolitan taxa in the flora. *Isoëtes*, *Juncus*, *Eryngium*, *Eleocharis*, and *Callitriche* are examples of genera that are associated with wetland habitats of many types in far-flung locations. In *Isoëtes* and *Eryngium*, as in *Branchinecta* and *Streptocephalus*, the genera are widespread but there are species endemic to the California vernal pools. The pattern is one of basic adaptive complexes persisting over long times and spinning off locally adapted endemic species as landscapes and climates create regions in which temporary waters become a significant habitat persisting long enough for speciation to occur.

Factors affecting assemblages of animal communities may be different than those affecting plant communities. In one study it was found that species richness of microcrustaceans and other

zooplankton was most strongly correlated with duration of inundation (phase ii). In contrast plant species richness was most closely associated with pool size (Ebert and Balko, 1987). The extreme diel changes in pool chemistry (Figure 2) raises interesting physiological questions, yet to be addressed. The remarkable change in water pH of 3 - 4 pH units over a period of hours potentially represents a significant stress to these organisms, although the weak buffering capacity of the water may minimize such pH effects.

At higher taxonomic levels, the specialization and the degree of restriction to vernal pools of the fauna seems to decrease with increasing body size. There appear to be few insect endemics restricted specifically to vernal pools and vertebrate species, though they utilize vernal pools, also exploit other aquatic habitats. Two amphibians, the California Tiger Salamander (*Amystoma californiense*) and the Western Spadefoot Toad (*Scaphiopus hammondii*) appear to be among the species most dependent on vernal pools (Keeler-Wolf et al., 1995).

REGIONAL AND WORLDWIDE DISTRIBUTION OF VERNAL POOLS

"California" Vernal Pools

Not strictly Californian, these vernal pools range over 1800 km from eastern Washington (~47°N) (Crowe et al., 1994) to northern Baja California (~31°N) (Moran, 1984). Despite numerous occurrences throughout this range, the extant vernal pools represent a small fraction (<10%) of those prior to recent anthropogenic alteration of these landscapes (Holland, 1978). Pools are distributed at low elevations, mostly below a few hundred meters although some occur over 1500 m (Keeler-Wolf et al., 1995). Within this broad range, they are found in a variety of settings, including grasslands, savannas, open chaparral and other scrubland. Floristically, pools vary greatly in composition and factors such as water duration and soil type commonly have been invoked to account for patterns (Holland and Jain, 1984; Zedler, 1987; Bauder and McMillan, 1998). For most large vernal pool plant genera, e.g., *Downingia*, *Orcuttia*, *Plagiobothrys*, etc., there tends to be a latitudinal replacement of species. At higher elevations seasonal pools take on a somewhat different aspect, as the length of summer drought decreases there tends to be an increase in perennial sedges and rushes capable of persisting through the dry period.

Vernal Pools in Other Mediterranean Climates

The climatic factors contributing to formation of vernal pools are present in the other Mediterranean climate regions of Chile, South Africa, Australia and the Mediterranean Basin. Except for Australia, however, there is relatively little evidence in the literature that temporary pools are prominent features of these regions. More information is becoming available, which does establish that vernal pool habitat does occur, but much is still unknown about the nature and extent of these wetlands.

Chile. Vernal pools in central Chile have been mentioned in descriptions of Chilean species of *Navarretia* (Crampton, 1954), *Blennosperma*, and *Lasthenia* (Ornduff, 1963) and in discussions of long distance dispersal (Raven, 1963). Recently we (J. Keeley, P. Zedler, S. Bliss, and M.K. Arroyo) have been conducting extensive studies of vernal pools in Chile and can report that they are widely distributed in the coastal region and central valley of Chile. They extend over 1000 km from interior valleys around Temuco (~39°S) in the south to the northern coastal desert region near La Serena (~30°S). Widely distributed throughout this range we have mapped over 25 distinct vernal pool areas with perhaps 100 pools in total, a remarkable number in light of the widespread and long term intensive land use throughout that region. As in California, pools appear to have developed over cemented hardpans, clay lenses and lava flows. The phenological behavior of the Chilean pool flora closely follows that observed in California. These pools are rainfed and the unbuffered nature of the water chemistry shows a diel flux in carbon dioxide and pH similar to that in California vernal pools. Additionally, *Isoëtes* and *Crassula* species occur in these pools and have CAM photosynthesis.

There are marked similarities and marked differences between the vernal pool floras of Chile and California (Table 3). Floristically, Chile and California are quite similar in possessing many of the genera of cosmopolitan aquatics, and some species, e.g., *Pilularia americana* Braun, *Callitriche verna* L., *Crassula solieri* (Gay) Meigen, *Elatine chilensis* Gay, *Lilaea scilloides* (Poir.) Haum., *Myosurus apetalus* Gay, *Ranunculus aquatilis* L., and *R. bonariensis* Poiret occur in both regions. Also, as in California there are a number of narrowly restricted pool-endemic taxa, specialized to the vernal pool environment. These Chilean vernal pool endemics, however, are far fewer in number than in California (perhaps by an order of magnitude) and five of the genera are represented by a single species in Chile. Most of these genera also occur in California vernal pools. *Downingia pusilla* and *Psilocarphus brevissimus*, are common to both regions, and three others *Navarettia involucrata* R. et P., *Blennosperma chilense* Less., and *Lasthenia kunthii* (Less.) H. et A. are very closely related to California species.

Thus, while we can conclude that Chile has vernal pool ecosystems similar to those of California, they differ in diversity and apparently in origin of the flora. California vernal pool specialists evolved from diverse genera well represented in adjacent terrestrial communities. It appears that many of the Chilean vernal pool specialists are descended from California taxa (many of which were likely vernal pool species), in all likelihood transported from north to south by long distance dispersal (e.g., Raven, 1963). One prediction from this amphitropical origin hypothesis is the expectation that the Chilean vernal pool spe-

TABLE 3. Chilean vernal pool plant genera (from Zedler, Keeley, Bliss, and Arroyo, unpublished). A = annual, P = perennial.

Cosmopolitan Aquatics	Vernal Pool Specialists
Lycophyta/Pterophyta	Anthophyta – Dicots
Isoetes (P)	*Blennosperma* (A)
Marsilea (P)	*Cardamine* (A)
Pilularia (P)	*Downingia* (A)
	Eryngium (P)
Anthophyta – Dicots	*Lasthenia* (A)
Callitriche (A)	*Navarretia* (A)
Crassula (A)	*Plagiobothrys* (A)
Elatine (A)	*Psilocarphus* (A)
Hydrocotyle (P)	
Myosurus (A)	
Ranunculus (A,P)	
Anthophyta – Monocots	
Eleocharis (P)	
Lilaea (A)	

cialists should be small-flowered autogamous species, since such a breeding system increases the probability of a single successful migrant producing offspring. While we can not say yet that the Chilean species are autogamous, they uniformly have flowers that are smaller than those of the outcrossing California progenitors (Bliss et al., 1998). This is well illustrated by *Downingia*; some California vernal pool species have flowers 2-3 cm in size in contrast to the Chilean species with flowers 2-3 mm (McVaugh, 1941). The Chilean *Blennosperma* and *Lasthenia* species illustrate a similar pattern, and are known to be self-compatible, unlike many of their Californian counterparts (Ornduff, 1963). Diminutive flowers on these and other Chilean vernal pool species fail to generate the spectacular floral displays of California pools, which may account for why this ecosystem has gone unrecognized for so long.

South Africa. Much of the Cape Region is composed of very sandy soils derived from sandstone and granitic substrates and lacks any subsurface impervious layer that would generate a perched water table. Nonetheless, either due to subsurface rock outcrops blocking drainage or a layer of clay, seasonal pools known locally as "vleis" or "pans" develop (Hutchinson et al., 1932; Campbell et al., 1980). Although drainage is inhibited, in many instances it must be significant because such pools are often short-lived (Keeley and Zedler, unpubl. obs.). Away from the coast, soils are more diverse and on some sites a clay duripan develops, giving rise to longer-lived vernal pools. In addition, pools are frequent in depressions that form in granite outcrops, such as west of Stellenbosch.

These pools have a number of widespread aquatic genera such as *Isoëtes* L., *Marsilea* L., *Aponogeton* L., *Crassula* L., *Callitriche* L., *Elatine* L., *Eleocharis* R.Br., *Potamogeton* L., *Ranunculus* L. and *Limosella* L. (Stephens, 1929; Keeley, unpubl. data). Some pools have endemic species of *Oxalis*, such as *O. disticha* Jacq. and *O. natans* L.f. and *Romulea aquatica* G. Lewis, which appear to be restricted to pool basins (R. Ornduff, pers. comm.). Pennell (1935, cited in Thorne, 1984) noted that *Chamaegigas* Dinter ex Heil., a diminutive annual in the Scrophulariaceae, is restricted to granite outcrop pools and that it was remarkably similar to another member of that family, *Amphianthus* Torr. from granite outcrops in the southeastern U.S (see discussion below). Detailed studies of the granite outcrop pools reveals a number of similarities with California pools, including low conductivity and a marked diel change in pH and CO_2. In addition, as with the California taxa, *Isoëtes* and *Crassula* species have well-developed CAM photosynthesis, whereas *Callitriche*, *Elatine*, *Eleocharis*, and *Ranunculus*, as in California, do not (Keeley, unpubl. data).

Western Australia. The landscape and floristic similarity between South Africa and Western Australia is well known and there appears to be a similar pattern of vernal pools on granite outcrops in both regions (Thorne, 1984; Ornduff, Zedler and Keeley, unpubl. obs.). The Western Australian granite outcrop pools, known as "gnammas" are similar to the South African pools in that they are often dominated by indigenous species of *Isoëtes* and non-native *Crassula* (which also have CAM photosynthesis, Keeley, 1982; Keeley and Morton, 1982). These pools share many of the physico-chemical features noted for California pools and many of the same ephemeral invertebrates (Bayly, 1982).

These gnammas and other Western Australia vernal pools have communities assembled from both cosmopolitan taxa (*Isoëtes*, *Marsilea*, *Pilularia*, *Aponogeton*, *Myriophyllum* L., and non-native *Callitriche*) and endemics derived from the local flora (Smith and Marchant, 1961; Thorne, 1984; S. Hopper, pers. comm.). Some widespread genera such as *Isoëtes* have radiated extensively in these vernal pools (Johnson, 1994). Similar to the Western Australian pools are temporary wetlands in the Mediterranean climate area of southeastern Australia (Lake et al., 1989). These pools posses a diverse fauna but the flora seems not to be as endemic-rich as those in the west.

Southwestern Australia has a rich diversity of other seasonally inundated wetlands on other substrates and these are referred to as "sumplands" (Hill et al., 1996). Many of these share features with California vernal pools in that they form on clay or carbonate mud with an impervious duripan and fill by direct precipitation. Others, however, lack a duripan and fill from rises in the water table. Recent work by Neil Gibson and Stephen Hopper (Hopper, pers. comm.) has found that it is only in the vernal pools with an impervious duripan that endemic seasonal

aquatic plants have evolved. They list 22 aquatic species that are strict vernal pool endemics, including (in addition to those noted above) dicots such as *Glossostigma* Wight & Arn. ex Arn., and *Hydrocotyle* L., and monocots such as *Amphibromus* Nees., *Hydatella* Diels., *Ottelia* Pers., *Schoenus* L., and *Wurmbea* Thunb. Other species distributed near the margins, and subjected to briefer periods of inundation, number in the hundreds.

Mediterranean Basin. There is little current or historical evidence of extensive pool ecosystems in this region. This is surprising in light of the presence of a Mediterranean climate, diversity of substrates throughout the basin, and widespread occurrence of landscapes conducive to vernal pool formation. Is it possible that millennia of intense grazing and agriculture have decimated such habitat? This may not be too far-fetched because vernal pool landscapes are more readily exploited than more rugged terrain; for example, in California it took just 200 years to decimate over 90% of such habitats (Holland, 1978). Perhaps less subject to exploitation would be pools in montane sites, as colleagues have reported observing seasonal pools in the mountains of northern Morocco (R. Ornduff, pers. comm.) and northern Spain (S. Bliss, pers. comm.). A number of papers have been written on temporary wetlands in the western Mediterranean Basin (e.g., Grillas, 1990; Bonis and Lepart, 1994; Serrano and Toja, 1995), but they appear to deal with ephemeral wetlands in flood plains draining relatively large watershed systems, and thus do not fit our definition of a vernal pool.

In the eastern Mediterranean Basin, seasonal pools commonly form on the coastal plain of Israel (G. Ne'eman, University of Haifa, Oranim, pers. comm.). These pools differ from California vernal pools in time of filling; autumn and early winter and the term "brumal pools" has been recently suggested for such winter pools (S. Schwartz, University of Haifa, Haifa, pers. comm.). Lack of scientific interest in these habitats suggests they lack a significant endemic flora, which may derive from the timing of pool filling; winter inundation and spring drying may narrow the window of time for plant growth. The Mediterranean Basin does, however, have endemic species of *Isoëtes* and *Crassula* distributed in seasonal wetlands. Further suggestion that vernal pool habitat may have been present, and even widespread, at one time is the invasion of California by several Mediterranean plants, e.g., *Crypsis vaginiflora* and *Lythrum hyssopifolium*, which are largely restricted to vernal pools (Keeley, unpubl. data).

Vernal Pools in Non-Mediterranean Climate Regions

While the Mediterranean climate is conducive to vernal pool formation, it is apparent that vernal pools, as defined above occur, to a limited extent, elsewhere in the world.

Continental Climate Granite Outcrop Pools. Stone Mountain, on the outskirts of Atlanta Georgia, is the southeast's equiva-lent of Mt. Rushmore. In addition to the likeness of Robert E. Lee (and other southern heroes) carved into the face of this massive stone, there are many depressions across the top of the mountain that fill each winter from rain and snow. These pools dry down in mid- to late spring and remain dry through to autumn. The pools that form on these rock outcrops have a wetting and drying cycle similar to California, despite being under a summer-rain climate; pool depressions remain dry throughout the summer due to evaporative demand coupled with thin soil substrates overlying impervious granite. In the southeastern U.S., vernal pools are restricted to these outcroppings, which locally are known as "granite outcrops." This rock formation occurs in scattered locations throughout the piedmont of Georgia and adjacent states (McVaugh, 1943).

Although granite outcrop communities have been the focus of a number of studies, we are unaware of any study focusing on the pools themselves. As is the case with California vernal pools, these granite outcrop pools have several endemic species of *Isoëtes* (with CAM photosynthesis) growing submerged in, and often dominating, the pools (Burbanck and Platt, 1964; Rury, 1978; Keeley, 1982). Annual *Crassula*, typical of most seasonal pools throughout the world, is replaced by the diminutive annual Crassulaceae *Sedum smallii* (formerly *Diamorpha cymosa*), whose distribution is described in "Manual of the Vascular Flora of the Carolinas" as "In and about vernal pools on flat granite outcrops" (Radford et al., 1964). Unlike *Crassula* species in other vernal pools *Sedum smallii* seldom grows submerged, rather occurs around the edges of these pools and does not have CAM photosynthesis (Keeley, 1998b).

A*mphianthus pusillus* (Scrophulariaceae) is a rare endemic annual and a true aquatic occurring in many of these granite outcrop pools. It germinates in the spring, but only during certain wet years. It produces a submerged rosette followed shortly afterwards by two floating leaves. Two flower types are produced, basal submerged flowers, which are cleistogamous, and scape flowers produced at the terminus of the scape and exposed to air (Hilton, 1993). Besides the *Isoëtes* species, there are few other aquatic vascular plants in these pools (Lammers, 1958) and thus *Amphianthus* will often dominate (Figure 3).

Granite outcrop pools of the southeastern U.S. are functionally quite similar to California vernal pools, and have endemic aquatic macrophytes specialized for these habitats. The granite outcrop pools, however, are floristically depauperate compared to California. One reason why granite outcrops might not have evolved a rich and diverse flora is that there is a very narrow window of time for plant growth. As in California, pools fill in winter but the cold temperatures typical of this continental climate precludes winter plant growth. Having lived in Georgia, one of us (JEK) can attest to the fact that spring is often very short and the climate passes quickly from cold winter temperatures to high summer temperatures, which rapidly dry out pool

FIGURE 3. Vernal pool dominated by *Amphianthus pusillus* on Heggies Rock in eastern Georgia, U.S.A., during early spring (photo by J. Keeley).

basins. It is for this reason that *Amphianthus pusillus*, one of the few specialized vernal pool species, is capable of completing its life cycle in as little as three weeks (Hilton and Boyd, 1996). Historical factors could also play a role since, unlike California, this region is not rich in genera of annuals. The granite outcrops themselves, however, seem to have evolved a significantly higher proportion of annuals than is typical for the region (Phillips, 1982). In the literature one can find passing reference to similar rock pools in other parts of the world.

Tropical Alpine Seasonal Pools. On high plateaus throughout the Andes Range of South America are seasonal pools that fill during the rainy season (Keeley, pers. obs.). These pools share a number of floristic characteristics with California vernal pools. Namely, they are generally dominated by various combinations of cosmopolitan aquatic taxa such as *Crassula*, *Callitriche*, *Elatine*, *Eleocharis*, *Isoëtes*, *Lilaea*, *Marsilea*, and *Ranunculus*. Due to the complex climatic patterns across the range, these pools fill and dry at different times and thus are not predictably "vernal" in nature. In terms of the cosmopolitan aquatic flora, these pools have most of the same genera as California vernal

pools. Ephemeral pools with a similar complement of these cosmopolitan genera are known from temperate latitudes as well (e.g., Slater et al., 1991). All such ephemeral pools, however, lack a specialized endemic flora, which makes them quite different from the California vernal pool ecosystem.

Other Seasonal Pools Not Considered To Be "Vernal Pools"

Because of their apparent similarity to vernal pools, we discuss two other seasonal pool habitats, but contend that they deviate significantly enough to be excluded by our definition of vernal pools.

Desert Playas. Playas, large shallow basins that hold water at irregular intervals, are a feature of arid regions throughout the world. These mostly receive runoff from a significantly larger watershed than the typical vernal pool. In the literature there is not always a clear distinction between large vernal pools and playas, as evident by the map of playas in (Hill, 1984) which shows some sites, such as Buena Vista or Tulare in the San Joaquin Valley, that are normally claimed by vernal pool ecolo-

gists. Perhaps due to the irregular or highly ephemeral nature of these pools, they do not seem to have evolved an endemic flora. One noteworthy exception is a playa on the Magdelena Plain near the southern tip of Baja California Sur. This temporary pond is the only recorded site for *Tuctoria fragilis* (Swallen) Reeder, the single member of the Orcuttieae not endemic to California vernal pools (Reeder, 1981).

An additional factor accounting for the general lack of an endemic playa flora is that the pools form during winter, when the cold continental climate is not conducive to plant growth, thus limiting plant growth during inundation. Also, due to excessive evaporative demand, and the fact that playas are typically in closed basins, salts often accumulate, leading to high salinity and alkalinity. Thus, tolerance of salinity is a requisite characteristic of much of the flora. Not surprisingly, Chenopodiaceae, a family also prominent in coastal estuarine habitats, is important in playas.

We, therefore believe that there are a number of key features of desert playas that separate them from vernal pools, as we define them. The most important are that the bulk of water in these pools is usually collected from a large drainage area, playas often are filled when temperatures are unsuitable for plant growth, and finally they are often saline or alkaline.

Great Plains Buffalo Wallows and Prairie Playas or Potholes. Rain-filled depressions in the Great Plains of the U.S. have long been known as buffalo wallows or hog-wallows, terms applied early-on to California vernal pools (Brandegee, 1890; Hoover, 1937; Crampton, 1954). These depressions are created when buffalo (*Bison bison*) trample the grassland vegetation and roll in the exposed ground, resulting in depressions from a few cm to a meter or more in depth (Polley and Collins, 1984). Due to soil compaction by the buffalo, these depressions retain water for several weeks during the growing season, creating ephemeral pools. Being more pervious than California vernal pools, standing water in buffalo wallows is consequently more ephemeral. Prairie playas are larger pools (average 6.3 ha) created by a clay lens and are a major feature of the landscape (> 20,000 in northern Texas and New Mexico, Bolen et al., 1989; Steiert, 1995).

Due to the summer rain climate of the Great Plains these pools may remain filled during late spring and summer. When they dry, the deeper soils retain substantially greater moisture than the surrounding grasslands (Polley and Wallace, 1986), which contrasts with California pool basins that dry down to soil moisture levels indistinguishable from those in the surrounding grassland (Zedler, 1987).

Thus, the underground organs of perennial aquatic species can persist in the seasonal pools of the Great Plains, and this is reflected in the dominance by widespread aquatic taxa (Correll

and Correll, 1972). These pools also have a much greater proportion of perennial species than in California vernal pools, very little endemism (Table 4), and a great deal of floristic overlap with the surrounding grasslands (Hoagland and Collins, 1997).

CONCLUSIONS

Seasonal pools are widespread in most parts of the world. Vernal pools are a more narrowly defined subset of these wetlands and, although widespread in California, are not unique to this region. Vernal pools occur in most other Mediterranean climate regions of the world and to a limited extent in other climatic zones. Despite the widespread distribution of vernal pool habitat, California appears to be the only region that evolved an extensive flora endemic to vernal pools. The reasons for this are not entirely clear. The spatial distribution of landscape features conducive to pool formation, coupled with the climate, has resulted in a region where pools once were far more extensive than most, if not all, other regions of the world. The metapopulation consequences of this pattern may have been critical to the evolution of the flora. Phylogenetic history may also be another important factor since the annual habitat is highly favored in vernal pools and the terrestrial California flora is dominated by many annual-rich families that appear to have been the source of many vernal pool endemic species.

TABLE 4. Plant taxa typical of mid-western buffalo wallows and prairie playas (from Polley and Wallace, 1986; Bolen et al., 1989). A = annual, P = perennial.

Buffalo Wallows	Playas

Pterophyta
  Marsilea mucronata (A)
	Anthophyta – Dicots
	  Polygonum spp. (A,P)

Anthophyta – Dicots
  Bacopa rotundifolia (A,P)
  Coreopsis tinctoria (A)
  Plantago elongata (A)
  Tridens albescens (P)
	Anthophyta – Monocots
	  Echinochloa crusgalli (A)
	  Potamogeton spp. (A,P)
	  Scirpus spp. (P)
	  Typha domingensis (P)

Anthophyta – Monocots
  Alopecurus carolinianus (A)
  Cyperus acuminatus (P)
  Echinochloa crusgalli (A)
  Heteranthera limosa (P)
  Juncus interior (P)
  Eleocharis spp. (P)	

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