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Edited by

Douglas G. Alexander and Robert A. Schlising

Department of Biological Sciences
California State University, Chico

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Accuracy of a Hydrogeomorphic Guidebook for Functional Assessment of Vernal Pools in Southern California

ANDREW J. BOHONAK AND ELLEN T. BAUDER

Department of Biology, San Diego State University
5500 Campanile Drive, San Diego, CA 92182-4614
bohonak@sciences.sdsu.edu

ABSTRACT. Vernal pools constitute a unique set of temporary wetlands that perform a variety of biotic and abiotic functions throughout California. Because nearly all vernal pool habitat historically present in Southern California has been lost to urbanization, there is a critical need to develop tools for assessing and monitoring the function of those pools that remain. Here, we review the methods used to produce models of functional capacity in a recent Hydrogeomorphic (HGM) Guidebook for Southern California's vernal pools (Bauder et al., 2009). This guidebook describes protocol for estimating Functional Capacity Indices (FCIs) in four functions: Surface and Subsurface Water Storage, Hydrologic Networks, Maintenance of the Characteristic Plant Community, and Maintenance of the Characteristic Faunal Community. It includes FCI models that directly estimate these four functions, as well as indirect FCIs for rapid assessment during either the wet or the dry phase. We found that direct FCIs, indirect FCIs and *a priori* FCIs based on expert opinion were highly and significantly correlated in nearly all cases. For regressions of indirect FCIs vs. direct FCIs, r^2 values ranged from 0.44 to 0.76, equal to or exceeding the accuracy of many other rapid assessment methods for temporary wetlands. We hope that the methodological outlines presented here will improve the transparency and accuracy of HGM guidebooks and similar approaches. Field applications of these assessment models will prove to be useful in vernal pools that are protected, proposed for loss, and utilized for mitigation in Southern California.

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INTRODUCTION

Temporary wetlands support a wide variety of ecosystem services, biotic resources, and societal needs. The hydrologic functions that they serve are the most obvious, as they periodically mediate the storage and movement of water both above and below ground. The biphasic nature of the habitat (alternating wet and dry phases) also dictates the biological functions that they perform. Although some organisms opportunistically use temporary wetlands when they hold water, others have evolved adaptations that allow them to persist through the dry phase as well. Extreme variation in hydroperiod, temperature and exposure to a variety of predators and diseases has made these habitats hotspots for adaptive evolution and speciation (Stebbins, 1976; Williams, 1987; Baskin, 1994).

California's vernal pools constitute its most unique and diverse set of temporary wetlands. The range of geographic settings, soil profiles and climates that support vernal pools produce significant variation in hydrologic regimes, particularly in terms of the length and predictability of ponding events. As a result, these ecosystems are known for high species diversity, endemism and abundant speciation within many plant and animal genera (Ornduff, 1976; Stebbins, 1976; Griggs and Jain, 1983; Baskin, 1994; Bauder and McMillan, 1998; King, 1998; Simovich, 1998; Ripley and

Simovich, 2008). Due primarily to habitat loss, many vernal pool species are federally or state listed as endangered or threatened. The vernal pools of Southern California have been particularly impacted, as it is estimated that more than 95% of pools historically present in this region have been lost (Bauder and McMillan, 1998). Those pools that do remain are generally isolated within small parcels, with the exception of military lands. Their long-term persistence is threatened by continued urbanization, periodic environmental catastrophes (like wildfires), and climate change. For example, climate predictions suggesting warmer, higher precipitation in California (Snyder et al., 2002) would drive many ephemeral wetlands toward longer, more frequent inundation events (Pyke, 2004). This could increase temperatures and inundation periods beyond species tolerances, or catastrophically alter intraspecies dynamics (e. g., see Schnei-der and Frost 1996; Bauder, 2005; Brooks, 2009). Consequently, there is a critical need to monitor both the biotic and the abiotic functions that vernal pools in Southern California perform.

As elsewhere, the mandate to inventory, monitor, conserve and manage vernal pool resources in this region does not fall within a single governmental jurisdiction. Rather, cities, counties, military installations and other federal agencies all assume responsibility for particular sites or particular functions that vernal pools perform. Most of the remaining vernal pool habitat in San Diego County falls within land owned by the military (Marine Corps Base Camp Pendleton, Marine Corps Air Station Miramar) or the City of San Diego, which has performed an extensive inventory of its sites (City of San Diego, 2005). With regards to both conservation and monitoring of function, there is a complicated set of relationships between these and other landowners, the regional planning agency (SANDAG), the regional landscape-level conservation plan [San Diego Multiple Species Conservation Program (MSCP), 1998, Franklin et al., 2011), the U.S. Fish and Wildlife Service (Bauder et al., 1998; U.S. Fish and Wildlife Service, 2003], the California Department of Fish and Game, conservation organizations and other stakeholders.

Bauder and colleagues began work on an HGM (Hydrogeomorphic) Guidebook for assessing vernal pool function in Southern California in 2000, completing it in 2009 (Bauder et al., 2009, hereafter referred to as the "vernal pool guidebook"). The HGM approach consists of a collection of concepts and methods for developing functional indices, and subsequently using them to assess a wetland's capacity to perform functions relative to similar wetlands in the region (Smith et al., 1995). HGM was originally designed to be used with the Clean Water Act Section 404 Regulatory Program permit review process.

The original goals for the method (e. g., assess and minimize project impacts, determine mitigation requirements) have been expanded to include evaluation of wetland management techniques, evaluation of both natural and restored wetlands, and provision of feedback for adaptive management and conservation plans. Approximately 20 regional and 2 national HGM guidebooks have been developed to assess function in a variety of wetlands (U.S. Army Corps of Engineers, 2010). Development of this particular HGM guidebook was overseen by the U.S. Environmental Protection Agency, Region IX. It follows the format outlined in a National Action Plan (National Interagency Implementation Team, 1997) and elsewhere (Smith et al., 1995; Butterwick, 1998; Smith and Wakeley, 2001; Wakeley and Smith, 2001; Noble and Carpenter, 2009). A complete summary of the HGM approach can be found in these publications, and a brief glossary of the terms used in HGM assessment is provided in Table 1.

TABLE 1. Terms and definitions use in HGM guidebooks and other wetland assessment methods (see Appendix A in Bauder et al., 2009; and Bohonak and Bauder, *in revision*).

Term	Definition
Reference Domain	Geographic area for which the assessment method is intended to be used, containing all of the reference pools. For the vernal pool guidebook (Bauder et al., 2009), the reference domain consists of coastal mesa / pedogenic pools, inland valley / pedogenic and alluviated pools, coastal mesa / landslide pools, and inland valley alluviated pools found in San Diego County, southern Orange County and southern Riverside County.
Reference Pools	The group of pools used to develop the assessment models. This group should encompass the known range of variability in natural processes, and the intensity and type of disturbances that are present. (See Table 3.)
Reference Standards	A subset of reference pools representing "the best" functional capacity in the reference domain. Reference standards perform characteristic vernal pool functions at a level that is as high as possible, and sustainable. Depending on the assessment method, reference standards will be assigned the maximum possible assessment score for at least one (and possibly all) functions.
Functional Capacity Index (FCI)	HGM assessment is based on the capacity of a wetland to perform functions. Capacity is scored as a Functional Capacity Index, on a scale from 0 to 1 that may be continuous or categorical.
***A priori* FCI**	An FCI score assigned to a reference pool for the purposes of model development, usually based on best expert opinion. The *a priori* FCI is most often a correlate of anthropogenic disturbance.
Anchor Pools	A set of pools used in initial FCI model development that includes the best (reference standards) and worst (lowest *a priori* FCI) pools in the reference domain.
Direct FCI	An FCI that is calculated using variables that are directly (i. e., mechanistically or functionally) linked to the functional capacity. These variables may be expensive to measure in terms of time, cost or expertise.
Indirect FCI	An FCI that is calculated using variables that are correlated with functional capacity, but not causally related to it. These variables can typically be assayed more quickly, inexpensively and with less expertise than those used in Direct FCIs.
Rapid Assessment Method (RAM)	An assessment method that can be conducted in a relatively short time. Indirect FCIs in the HGM framework are nearly always RAMs.
Validation	Evaluation of an assessment model using an independent evaluation of function. Indirect FCIs are often developed only using *a priori* FCIs, and later validated using direct FCIs. Alternatively, validation may be conducted with pools that were not used during model development.

The goal of this paper is to provide an overview of assessment model development for the Bauder et al. (2009) vernal pool guidebook. Using a large data set that spans multiple years for a large number of pools, we demonstrate that these models achieved a relatively high degree of accuracy (r^2 for indirect vs. direct estimates of function = 0.44-0.76). Together with Bohonak and Bauder's (*in revision*) review of specific technical issues associated with wetland assessment, we hope that this paper will improve the transparency and accuracy of HGM guidebooks and similar approaches.

METHODS

Scope of the Vernal Pool Guidebook

The vernal pool guidebook (Bauder et al., 2009) is based on data collected between 2000 and 2007 from reference pools throughout Southern California that represented a diversity of landscape settings and disturbance histories. The reference domain selected for this region includes five pool types: coastal mesa/pedogenic, inland valley/pedogenic and alluviated, coastal mesa/landslide and inland valley alluviated (see Chapter 3 in Bauder et al*.,* 2009). The vernal pool guidebook includes detailed descriptions of five major functions that vernal pools perform (Table 2). For four of the functions, statistical models are presented for assessing individual pools. We were unable to develop models for the fifth function (Biogeochemical Processes), because the data were unreliable due to technical laboratory problems.

The dependent (Y) variable in HGM assessment models is termed a Functional Capacity Index (FCI), with values ranging from 0 (no function) to 1 (maximum function expected in an undisturbed pool). The vernal pool guidebook presents FCIs for assessment of these four functions directly (when there has been sufficient precipitation), and also indirectly (using pool and landscape features that correlate with functional capacity, but are not directly related to it). Using the nomenclature presented by Bohonak and Bauder (*in revision*), models that directly estimate function are termed direct FCIs. Direct FCIs can be time-consuming and expensive to perform, since they require personnel with specific expertise and experience. The timeframe to collect data for direct FCI models is also constrained by seasonal and annual precipitation. Indirect estimates of function (termed indirect FCIs) can be performed at any time of year by a team of 1-2 researchers with a modest amount of training, usually with a site visit of 30 minutes or less. However, indirect FCIs should only be used when direct FCIs cannot be used. (Direct estimates of vernal pool function are not possible during the dry phase, or when there has been insufficient precipitation during the wet season to elicit functional responses.) Thus, indirect FCI models in the vernal pool guidebook constitute Rapid Assessment Methods (RAMs), according to the common use of this term in wetland assessment.

During development of the vernal pool guidebook, we collected direct and indirect measures of functional capacity for the first four functions listed above. For the function Hydrologic Networks, we treated entire hydrologically linked pool networks as the unit of observation (replicate) for data analysis. The other functions used individual vernal pools as the unit of observation, although some variables used in model development are network- and watershed-level attributes. Consequently, the vernal pool guidebook is designed for assessment of individual pools, and we do not recommend that each pool's score be weighted by its surface area. (Note that vernal pools within the reference domain tend to be relatively small and uniform in size, with surface areas < 300 m^2.)

Data were collected over a time period that consisted of one winter with average precipitation, two winters with abnormally low precipitation, and one summer following a rainfall year with average precipitation. After preliminary fieldwork, potential field sites were

TABLE 2. Descriptions of the functions included in the vernal pool guidebook (Bauder et al., 2009).

Function	Definition
Surface and Sub-surface Water Storage	Capacity of the vernal pool wetlands complex to capture and store precipitation falling on the basin and catchment area. Although moisture is stored both on the surface and in soils, only free water on the surface of the basins is assessed in the vernal pool guidebook.
Hydrologic Networks	Capacity of the hydrologic network (i. e., water bodies through which water moves to the local master stream) to be connected. The links include pools, the swales or subsurface flowpaths that connect them or the drainages of various types through which flows move into the master stream. Only surface connections are assessed in the vernal pool guidebook.
Maintenance of the Characteristic Plant Community	Capacity of the wetland habitat to support persistent populations of plant species characteristic of vernal pools in Southern California.
Maintenance of the Characteristic Faunal Community	Capacity of the vernal pool to provide food, cover, and reproductive opportunities for animal taxa for which these wetlands are essential for some or all parts of their life cycle.
Biogeochemical Processes	Capacity to remove imported nutrients, contaminants, and other elements and compounds through biotic and abiotic processes, and to convert and recycle elements and compounds from one form to another. Hydrology, soil structure and composition and vegetation are the key determinants of biogeochemical processes in vernal pools.

narrowed to 61 vernal pools spanning a range of disturbance types and levels from across the reference domain. Variables that were used to directly measure functional capacity are listed and defined in Appendix B in Bauder et al. (2009) and briefly summarized here:

- Surface and Sub-surface Water Storage: total length of inundation in a season, longest continuous inundation, number of times ponded, maximum depth,
- Hydrologic Networks: number of pools in the hydrologically connected pool network that continuously ponded ≥ 5 days, number of headwater pools that simultaneously held water, number of headwater basins that filled to their maximum depth at least once, total length of pool inundation in a season,
- Maintenance of the Characteristic Plant Community: species-level assessment of plant communities within and surrounding each pool (summarized individually and by functional groups), and
- Maintenance of the Characteristic Faunal Community: species-level assessment of crustacean communities within each pool (summarized individually and by functional groups).

Due to time and expense, these particular variables were measured for only a subset of the 61 pools in many functions (data column 2 in Table 3). However, all 61 pools were scored for approximately 40 additional field variables that might correlate with function (and thus be used for rapid assessment with the indirect FCI models). These indirect correlates of function (listed in Appendix B in Bauder et al., 2009) can be summarized in four general categories:

- Pool attributes (e. g., maximum length, maximum depth, presence and type of

cracks in the sediment),
- Local connectivity (e. g., presence of inlets and outlets, position in the network of connected pools),
- Watershed attributes (e. g., watershed size, presence of Mima mounds), and
- Disturbance (e. g., modifications to inlets and outlets, past and present land use in the watershed).

Analysis of Model Accuracy

Validation of HGM models consists of evaluating their accuracy by comparing FCI scores with an independent evaluation of function (Wakeley and Smith, 2001). (Depending on what data sets are used, this process may be more properly termed calibration or confirmation: Oreskes et al., 1994.) For example, assessment models often consist of an indirect FCI calibrated using an *a priori* FCI (the *a priori* FCI is usually assigned through best expert opinion, based on disturbance). In these cases, validation can be conducted with data that directly assess functional capacity, collected at a later date.

An ongoing process for validating the model and iteratively recalibrating it can be established by continuing to gather and analyze data from new pools, new seasons, and possibly new variables. But because validation does not often occur prior to HGM guidebook publication, most HGM guidebooks consist primarily of indirect FCI models or mixed direct/indirect models. This limitation is not unique to the HGM approach. Many wetland assessment methods (including the California Rapid Assessment Method, CRAM: Collins et al., 2008) consist of a Rapid Assessment Method that only indirectly estimates function, calibrated on disturbance. The added time and expense of directly estimating functions such as water storage capacity, or plant and faunal community composition, are often relegated to unspecified future studies.

Because we collected data simultaneously for *a priori* FCIs, indirect FCIs, and direct FCIs, our approaches to model validation and model calibration overlapped to some degree. As we describe below, validation was conducted in two ways. First, draft models for each direct FCI were developed using only the best and worst pools in the data set (see "anchor pools" below). Models were then validated using additional pools, and statistical fit was improved as the model was recalibrated (see sample sizes in data columns 1 and 2 of Table 3). Second, draft models for each indirect FCI were developed using a subset of the available pools, and then validated and recalibrated on a superset (data columns 3 and 4 of Table 3). The high correlations between the direct FCIs and indirect FCIs for each function presented here provide evidence that the indirect FCIs provide accurate estimates of functional capacity.

Assigning **a priori** *FCI Scores to Each Pool*

We formalized the process of calibrating functional capacity using best expert opinion by first assigning an *a priori* score of function (the "*a priori* FCI") to each pool for each function. To maintain objectivity, we developed verbal definitions for *a priori* FCI values of 0.00, 0.10, 0.25, 0.50, 0.65, 0.75, and 1.00 (Appendix D6 in Bauder et al., 2009; Bohonak and Bauder, *in revision*). The *a priori* FCI scores were made using the HGM team's best expert opinion, and tended to correlate with disturbance. Thus, *a priori* FCIs for the four functions were highly, but not perfectly, correlated (Pearson correlation coefficients 0.82-0.97). For example, a pool that has been hydrologically compromised to some extent may still maintain a fully functional faunal community. Practical issues surrounding the assignment of *a priori* FCI scores for hydrologically atypical pools are addressed by Bohonak and Bauder (*in revision*).

TABLE 3. Sample sizes for reference pools used to develop the assessment models. Entries indicate the number of vernal pools, except for Hydrologic Networks.

	Direct FCI development		**Indirect FCI development**	
Function	Preliminary: anchor pools	Validation/ Calibration	Preliminary	Validation/ Calibration
Surface and Sub-surface Water Storage	26	45	45	61
Hydrologic Networks	3 networks	7 networks	7 networks	24 networks
Maintenance of the Characteristic Plant Community	33	61	61	61
Maintenance of the Characteristic Faunal Community	21	28	28	61

Preliminary Direct FCI Model Development Using Anchor Pools

Analysis of each function began with development of a direct FCI model in DataDesk, v. 6.2.1 (Velleman, 1997). Exploratory data analysis was generally based on general linear models (GLMs) with individual pools as replicates, the *a priori* FCI as the dependent (Y) variable, and a suite of independent (X) variables that potentially assess the functional capacity directly. GLMs are standard statistical analyses in which the coefficients relating dependent and independent variables (which may be continuous or categorical) are arrived at by minimizing the sum of squared residuals. (This subsumes simple linear regression, multiple regression, ANOVA, ANCOVA, etc.) During exploratory data analysis, the initial set of X variables that directly measured function was expanded by data transformation and the creation of summary statistics. For example, quantitative variables such as pool depth were examined in scatterplots for evidence of linearity and threshold values. Some were transformed (e. g., log or square root transformation) in order to meet GLM assumptions, or scaled (i. e., converted into ordered categories). In the case of species presence/absence, we created composite variables such as the number of non-native species, or the number of "indicator" species that are characteristic of undisturbed vernal pools (see Characteristic Plant Community and Characteristic Faunal Community functions in Bauder et al., 2009).

The actual functional *response* of a vernal pool (as opposed to its potential *capacity*) depends on its maximum depth, its position in the landscape, and the precipitation patterns in any particular year (e. g., Ripley and Simovich, 2008; Bauder, 2011). Models that account for these factors will tend to provide a more accurate assessment of overall functional capacity. We included them in the following ways (see Bauder et al., 2009 for details):

- Maximum inundation depth was included as a factor in the *direct* FCI for Surface and Sub-surface Water Storage, Maintenance of the Characteristic Plant Community, and Maintenance of the Characteristic Faunal Community. Maximum inundation depth was included as a factor in the *indirect* FCI for Surface and Sub-surface Water Storage, and Maintenance of the Characteristic Faunal Community. Pools with a maximum depth < 7 cm cannot be scored for Maintenance of the Characteristic Faunal Community using either the direct FCI or the indirect FCI, because too few of these very shallow pools have been surveyed to develop accurate models.

- Landscape position was categorized as isolated pool, headwater pool, flow-through pool, or terminal/collector pool. This factor was included in both the direct FCI and the indirect FCI for Surface and Subsurface Water Storage. Two of the four variables in the direct FCI for Hydrologic Networks accounted for specific attributes of headwater pools.
- Annual variation in precipitation is particularly critical for directly assessing Surface and Sub-surface Water Storage. For this function, the primary HGM data set was supplemented with data from an additional 10 years (10-46 pools per year) that span a variety of total rainfall amounts and within-season patterns. The direct FCI for Surface and Sub-surface Water Storage included submodels for dry, average/above average and wet years (defined in Bauder et al., 2009).

Following standard HGM model development, the initial GLM for each function used only the "anchor pools" that represent the lowest functional capacity ($0.25 \geq$ *a priori* FCI ≥ 0.00) and the highest functional capacity (*a priori* FCI = 1.0, called "Reference Standards" in the HGM approach; Table 1). These statistical analyses typically included a mixture of continuous and discrete variables, and were iteratively improved through addition and removal of variables. Residual scatterplots and boxplots were continually re-examined for outliers and evidence of non-linearity, and additional X variables were tested. We began each new model by including interactions among X variables when they were logically defensible, and retained them when known processes could explain the sign and the magnitude of their effects. When models that included different sets of X variables provided similar statistical fits (i. e., r^2), we tended to retain models that would require less time to measure in the field, and/or were more likely to have less measurement error by different sets of researchers.

Calibration of Direct FCI Model Using all Pools

The preliminary FCI developed during the previous step was validated using additional pools and then recalibrated (see Table 3 for sample sizes). As the GLM was tested with the addition and removal of X variables, we tended to retain models in which scores for the anchor pools remained close to their *a priori* values. We believe that the labor-intensive process used to develop the preliminary model, validate it and recalibrate it was necessary. Although the final statistical model can be independently verified, it would be difficult to precisely replicate each of the preliminary analyses. Due to the nature of the data, it would be unwise to trust an automated procedure for HGM model development (such as forward stepwise addition) in the absence of expert opinion. The number of replicates (pools) is relatively low compared to a high number of potential X variables (especially in indirect FCI development: see below), and many of the X variables exhibit a high degree of co-linearity.

Estimates of Surface and Sub-surface Water Storage (e. g., maximum water depth, total number of days inundated per year) are dictated by rainfall patterns and amounts throughout the wet season. For added accuracy in this function, we supplemented the data set collected for the HGM project with an unpublished 20-year data set from Bauder (97 pools – 10-46 pools in any particular year, 18 of which overlapped with the HGM data set). Analyses of the 20-year data set suggested that precipitation patterns be divided into four categories:

1) Driest years: Seasonal precipitation < 14 cm: Function cannot be assayed directly.
2) Dry years:
    a) Seasonal precipitation between 14 cm and 17.5 cm, or
    b) Seasonal precipitation between 17.5 cm and 25 cm, when *less* than 50% of the total fell in the two months with the highest rainfall.
3) Average to above average years:
    a) Seasonal precipitation between 25 cm and 32 cm, or
    b) Seasonal precipitation between 17.5 cm and 25 cm, when *more* than 50% of the total fell in the two months with the highest rainfall.
4) Wet years: Seasonal precipitation greater than 32 cm.

Preliminary Indirect FCI Model Development: Calibration on Direct FCI

The initial set of X variables that indirectly measured function was expanded by data transformation and the creation of summary statistics as described above for direct FCI analyses. However, indirect models tended to have far more potential X variables than the direct models did: *circa* 40 initial variables represented direct field measurements, and an additional *circa* 45 variables were derived from these in a variety of ways. The Y variable in the indirect FCI GLM was the direct FCI score calculated using the equation developed in the previous step. All vernal pools for which direct FCI data were available were included.

As described above for the direct FCI, we also employed an iterative approach to indirect FCI development through the addition and removal of model variables, and repeated examination of residual scatterplots and boxplots. We considered whether the causal mechanisms that would underlie the sign and magnitude of variables that were statistically significant were logical.

Final Indirect FCI Model Validation

The suite of potential X variables for indirect FCI model development was available for 61 pools. For the function Maintenance of the Characteristic Plant Community, direct FCI data were also available for all 61 pools. For the remaining three functions, direct FCI data were only collected for a subset of the 61 pools (Table 3). In these cases, we conducted a final validation of the indirect FCIs using the *a priori* FCI. Because we consider the indirect FCI to be a poorer predictor of functional capacity than the direct FCI, we only made minor model adjustments (e. g., slight changes to model coefficients) after validation. If major model adjustments were suggested (such as removal or addition of a variable), we reverted back to the preliminary model development phase, and repeated the process.

RESULTS

The relationships between *a priori* FCI, direct FCI and indirect FCI for the four functions are depicted in Figure 1. Each point on the graphs represents a single pool, and sample sizes correspond to the Validation/Calibration columns in Table 3. Graphs in the first column in Figure 1 represent calibration of direct FCI on *a priori* FCI for each function. As summarized in Table 4, direct estimates of functional capacity correlated best with *a priori* FCI for the function Maintenance of the Characteristic Plant Community ($r^2 = 0.77$, $p \leq 0.0001$), followed by the Fauna and Water Storage functions ($r^2 = 0.21, 0.13$, $p < 0.02$) and the Network function ($r^2 = 0.23$, $p = 0.28$). The third column in Figure 1 represents calibration of the indirect FCI on direct FCI scores. Except for the Network function ($p = 0.11$), indirect FCIs correlated strongly with the direct FCIs ($p \leq 0.0001$ for the remaining three). The middle column shows relationships between

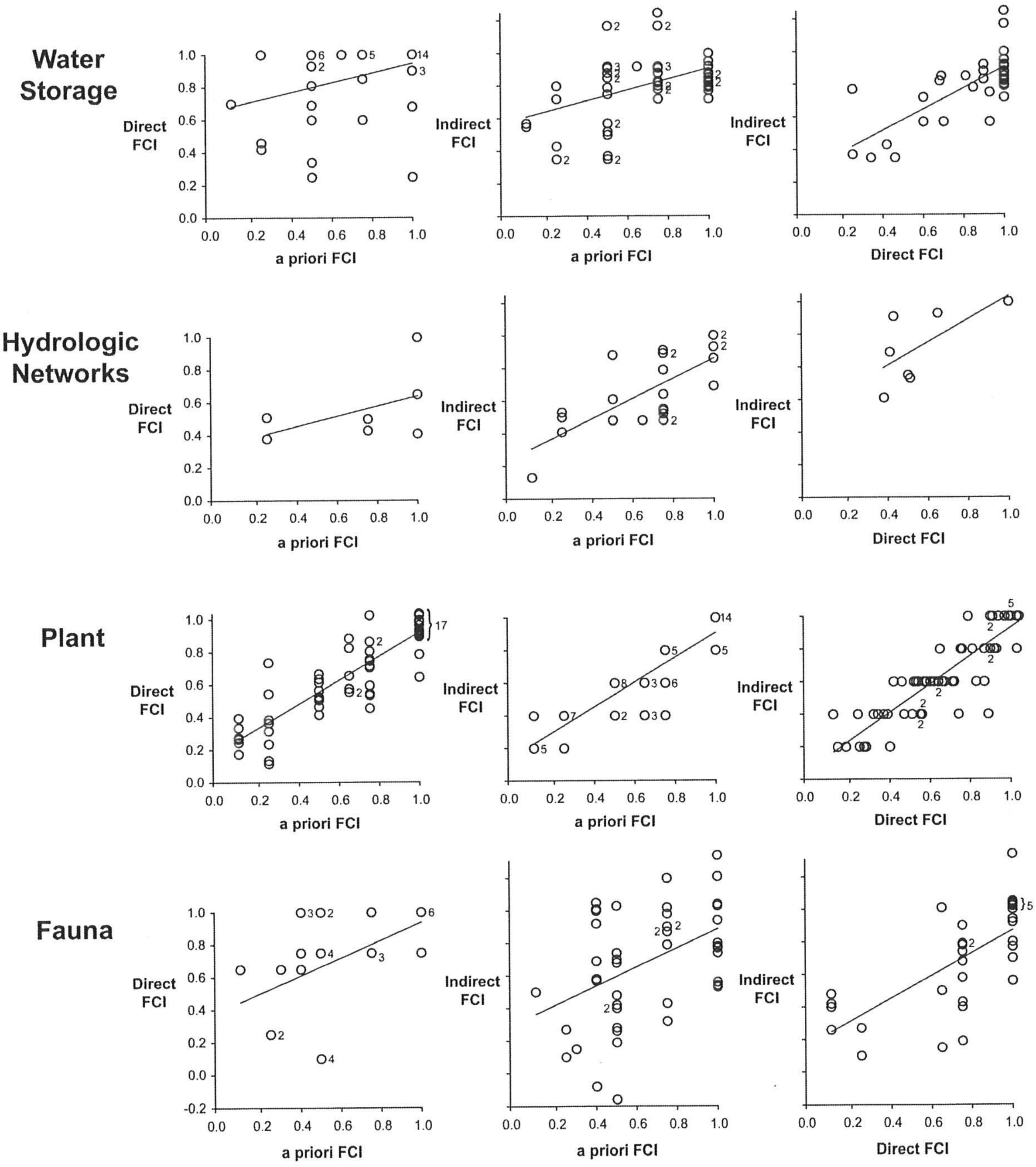

FIGURE 1. Scatterplots depicting the relationships between a priori FCI, direct FCI and indirect FCI for the four HGM functions. Lines represent simple linear regressions, and groups of overlapping points are denoted numerically.

indirect FCI and *a priori* FCI. These correlations were used in model validation/calibration for three of the four functions, and are high in all cases ($p \leq 0.0003$).

Overall, relationships between the three estimates of functional capacity tended to be linear for all four functions. Large outliers were rare and statistical fit in the twelve scatterplots was high, whether estimated nonparametrical-

TABLE 4. Summary of fit for assessment models. The two values represent the Spearman rank correlation coefficient (rho), and r^2 for the linear regressions depicted in Figure 1.

Function	**Direct vs. *a priori***	**Indirect vs. *a priori***	**Indirect vs. direct**
Surface and Sub-surface Water Storage	0.34, 0.13*	0.37, 0.20**	0.67, 0.52***
Hydrologic Networks	0.44, 0.23	0.72, 0.51***	0.68, 0.44
Maintenance of the Characteristic Plant Community	0.87, 0.77***	0.91, 0.82***	0.88, 0.76***
Maintenance of the Characteristic Faunal Community	0.47, 0.21**	0.37, 0.19**	0.73, 0.48***

$* \; p < 0.05$, $** \; p \leq 0.01$, $*** \; p \leq 0.0001$

ly (Spearman's rho = 0.34-0.91) or parametrically (average r^2 from regressions = 0.47; 10 of 12 were statistically significant at $p < 0.05$; Table 4). The two regressions that were not significant both included the direct FCI for Hydrologic Networks for which only seven data points (networks) were available (Table3). The most relevant analysis of fit regarding accuracy of the RAM FCIs in the vernal pool guidebook is the correlation of direct FCI vs. indirect FCI, which was high in all cases (Spearman's rho = 0.67-0.85, r^2 = 0.44-0.76).

DISCUSSION

It is obvious that habitat assessment should include direct metrics of biotic and abiotic functions whenever possible. Indirect estimates of functional capacity can never be more than an imperfect approximation. However, development, management, conservation and regulatory organizations often do not have adequate resources to directly estimate function. In addition, the timing of functional capacity assessment in temporary wetlands is constrained by the seasonality of the wet phase, and weather-driven variability in hydroperiod during the wet phase. For example, California's vernal pools are remarkable for a flora that is dominated by annuals and a fauna composed primarily of obligately aquatic invertebrates. Direct assessment of these species can only take place under a rather narrow set of moisture conditions, or in some cases, by hatching them from their dormant forms (i.e., seeds or cysts). Because inter- and intra-annual variability in precipitation amount and pattern can lead to oscillations in species abundance, long term studies are required to provide a full assessment of pool function (Bauder, 2000, 2011).

Direct assessment of hydrological functions such as Surface and Sub-surface Water Storage is also constrained by seasonal storm intensity and rainfall amount, neither of which can be predicted in advance. Pools (and networks of pools) may have the capacity to hold water for weeks (or rarely, months) and to be connected by surface flows, but in Southern California some pools only do so once or twice per decade (Bauder, unpublished data). This is particularly true of shallow headwater pools, which are often discounted but play an important role in catchment and landscape scale hydrology. In very wet years, headwater pools provide additional water storage and reduce the amount of water moving through and out of a network (Bauder et al.,. 2009).

Because resources are rarely available for long term, direct assessment studies, it is imperative that indirect measures of functional capacity provide accurate surrogates. We found that the accuracy of the indirect FCIs used in the vernal pool guidebook compares favorably to other RAMs. For example, Spearman's rho was 0.67-0.88 for indirect vs. direct FCIs (Table 4), compared to rho = 0.26-0.50 for a range of metrics used in the estuarine and riverine CRAMs in California (Stein et al., 2009). Similarly, our r^2 values of 0.44-0.76 are comparable to r^2 = 0.31-0.92 for regressions of various RAMs on a direct estimate of function in tidal wetlands (Wigand et al., *in press*), r^2 = 0.48-0.73 for metrics that describe floristic quality and landscape-level disturbance in depressional marshes (Cohen et al., 2004), and r^2 = 0.06-0.51 for regressions of bird species diversity metrics on a variety of disturbance-based RAMs (Stapanian et al., 2004).

We believe that unexplained error in the regressions depicted in Figure 1 is driven largely by inter-annual variation in precipitation patterns and hydroperiod. In support of this hypothesis, we note that correlation coefficients were lowest for Surface and Sub-surface Water Storage, for which direct estimates of functional capacity are dictated by recent rainfall events. In contrast, high correlation coefficients for Maintenance of the Characteristic Plant Community reflect the resilience of most vernal pool plants to prolonged drought. Apart from validating and re-calibrating the HGM models with new long-term monitoring studies (Bauder, 2011) their statistical fit can probably not be improved much without a loss of information. (For example, r^2 could be improved by converting both the direct and indirect FCI indices from continuous variables into 3-4 ordered categories.)

As recognized in USFWS recovery plans for vernal pools (Bauder et al., 1998; U.S. Fish and Wildlife Service, 2005), habitat restoration/enhancement is an important supplement to the conservation of existing high quality pools. Thus, assessment tools are needed for an array of sites that are protected, proposed for loss, and utilized for mitigation. The benefits and cost-effectiveness of these efforts can be vastly improved by considering the full array of functions that vernal pools perform, and monitoring them before, during, and after the restoration (or creation) process (Black and Zedler, 1998; Bauder, 2011). It is our belief that the assessment tools provided in the Bauder et al. (2009) HGM guidebook are the best currently available for Southern California's vernal pools, and that their accuracy and utility can be refined iteratively with future use.

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