Original Research Article

Indicator-species and coarse-filter approaches in conservation appear insufficient alone

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A B S T R A C T

Because resources are finite, conservation practices can be based on shortcuts (i.e., a quicker way to a desired outcome). For example, indicator species are often used as a shortcut to justify conservation at greater organizational levels (i.e., communities, ecosystems, landscapes). Conversely, "coarse-filter" approaches to protect landscapes are often assumed to conserve organizational levels nested within that landscape. But is conservation biology fundamentally different from other applied sciences, in which shortcuts appear rare or absent? To evaluate this question requires a rarity; much data across organizational levels in numerous well-defined systems. We used data collected in vernal pools (N = 61) in greater San Diego, California and seasonal wetlands (N = 70) in Florida. Data for plant species of concern, plant community diversity, ecosystem function, and landscape integrity were evaluated using partial least-squares structural equation models. Three *a priori* alternative models for each of the indicator species and coarse-filter approaches were tested, where models varied in complexity and included shortcuts between organizational levels. We found little support for shortcuts connecting distant levels, but species of concern and community diversity were always significantly and strongly interrelated. We conclude that species of concern often predict community diversity (and vice versa) but shortcuts between more distant organizational levels are hard to find. Given that study systems here were numerous, discrete and relatively small (i.e., well-described), we expect that effective shortcuts will be difficult to demonstrate for many other systems that do not share all those attributes. Thus we suggest that regional ensemble conservation goals and approaches will be more often effective than relying on assumed conservation shortcuts with little evidence.

1. Introduction

Potential "shortcuts" for conservation planning have been debated for decades, where a reliable shortcut would be a measurable quantity (e.g., landscape heterogeneity) that serves well as a surrogate for another measure of interest (e.g., population status of a species of concern; Noss, 1987; Lambeck, 1997; Simberloff, 1998; Morrison et al., 1998; Andelman and Fagan, 2000; Smallwood, 2000;
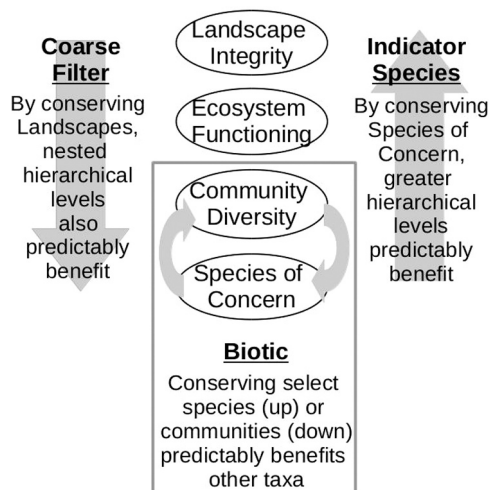

Fig. 1. Coarse-filter and indicator species conservation approaches. A coarse-filter approach predicts conservation benefits all the way down to species of concern. An indicator species approach predicts conservation of species of concern also benefits upper organizational levels. Biotic linkages (in the box) may also be expected among closely-related species and communities.
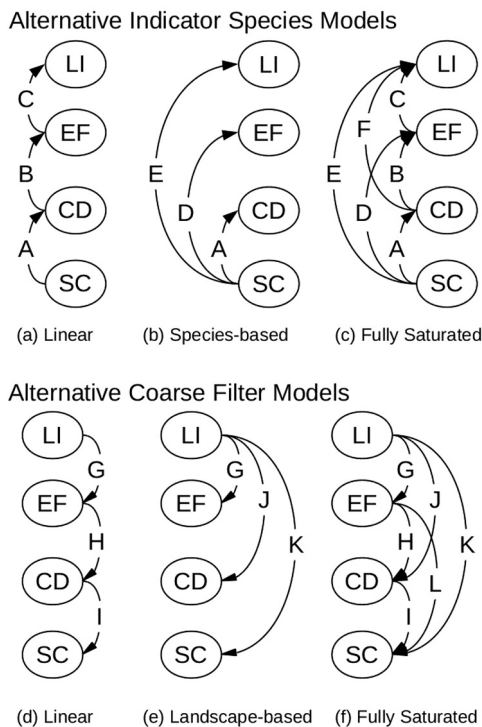

Fig. 2. Alternative hypotheses for indicator species and coarse-filter approaches, ranging from simple linear, bottom-up or top-down, and fully-saturated models. LI = landscape integrity; EF = ecosystem function; CD = community diversity; SC = species of concern.

Araújo et al., 2001; Brooks et al., 2004; Bonn and Gaston, 2005; Heino et al., 2005; Rodrigues and Brooks, 2007; Caro and O'Doherty, 1999; Grantham et al., 2010; Tingley et al., 2014). Why does conservation biology continue to search for reliable shortcuts, even as other applied sciences have concluded no shortcuts exist (e.g., Hydén, 1983; Berry, 2001; Brevini et al., 2010; Campbell, 2013)? The usual justification is limited resources (including expenses, expertize, and data), but other disciplines share this constraint. Conservation biology may either explore all management avenues (Tingley et al., 2014) or accede to demands for expedient shortcuts, whether or not they reach intended goals. Objective evaluation of empirical evidence may help resolve the best path.

Potential conservation shortcuts may be organized using hierarchical levels of organization, including species of concern (SC), community diversity (CD), ecosystem function (EF), and landscape integrity (LI; Fig. 1). Here we address two potential shortcuts *among* these nested hierarchical levels and that work in opposing directions; coarse-filter and indicator species approaches, discussed below (Fig. 1; Noss, 1987,1990). Conservation strategies focused *within* an organizational level are not addressed here, including fine-filter conservation efforts that target single species (Tingley et al., 2014), or cross-taxon shortcuts, where conservation of one species may benefit another species (Rodrigues and Brooks, 2007).

A coarse-filter approach (also known as "conserving nature's stage;" Beier et al., 2015) uses upper organizational levels (landscapes or ecosystems) as surrogates to predict outcomes for target taxa (Fig. 1; Noss, 1987, 1996; Thomas, 1996; Christensen et al., 1996; Araújo et al., 2001, Grantham et al., 2010; Januchowski-Hartley et al., 2011; Hermoso et al., 2013). The coarse-filter approach has been widely applied to millions of hectares in the USA (e.g., Thomas, 1996; Noss, 1987) and is prominent in climate change planning (Hunter et al., 1988; Beier et al., 2015; Lawler et al., 2015; Coffin et al., 2021).

Conversely, an indicator species approach focuses on species or communities, with an expectation that they signal integrity of ecosystems and landscapes (Noss, 1990; Rosenberg and Resh, 1993; Caro, 2010; Segura et al., 2014; Manning et al., 2015; Davis et al., 2020). Lower organizational levels in this approach predict the status of upper organizational levels (Fig. 1). For example, conservation of an indicator species in rivers with high water quality but absent from rivers of lesser water quality is likely to conserve high water quality sites. Select taxa and community diversity have been used as indicators of water quality for decades (Fausch et al., 1984; Rosenberg and Resh, 1993).

A subset of both approaches above exists, where shortcuts may be predictive between adjacent species of concern and community diversity (Fig. 1). We label this subset "biotic" here because it focuses on species and communities. For example, indicator, flagship, or umbrella species may predict diversity in and among communities, and in turn, community diversity may predict species of concern (Fig. 1; Lambeck, 1997; Simberloff, 1998; Andelman and Fagan, 2000; Lamoreux et al., 2006).

Here we evaluated three *a priori* alternative hypotheses for each of the indicator species (Fig. 2a–c) and coarse-filter approaches (Fig. 2d–f). The biotic approach was repeatedly evaluated because it is nested within each of the larger approaches (Fig. 2). Hypotheses ranged in complexity from a simple linear model to the fully-saturated (most complex) model, with intermediate hypotheses representing species-based or landscape-based approaches (Fig. 2).

In the linear hypotheses (Fig. 2a, d), each successive level predicts only the next in the nested hierarchy. These hypotheses assume effective stepwise shortcuts among adjacent organizational levels, but no functional linkages two or three organizational levels away. The biotic subset (Fig. 1) is also a pair of simple linear hypotheses.

The species-based and landscape-based hypotheses (Fig. 2b, e) are intermediate in complexity. The species-based hypothesis uses only the presence of species of concern (SC) to predict each of the other organizational levels. Species of concern may include endangered or threatened species, or those known to indicate habitat quality. Support for the species-based hypothesis indicates that SC offer a valuable and efficient shortcut with benefits at all organizational levels. The landscape-based hypothesis flows in the opposite direction (Fig. 2e), where landscape variables alone predict conservation benefits at all lesser levels in the hierarchy. Support for the landscape-based hypothesis indicates that protection of a landscape efficiently confers predictable conservation benefits on all other organizational levels.

Finally, fully-saturated hypotheses include all possible paths between organizational levels (Fig. 2c, f). This complexity may better reflect complex natural systems, even if some paths are statistically insignificant within an otherwise operational model. Support for a fully-saturated hypothesis indicates conservation benefits at "downstream" organizational levels are the complex products of outcomes at "upstream" levels.

The above hypotheses (Fig. 2) are well-suited to structural equation models (SEMs), which test networks of cause-effect relationships in conservation biology and many other disciplines (e.g., Grace, 2006; Harrison et al., 2006; Grace et al., 2012, 2016; Hermoso et al., 2013; Stival dos Santos et al., 2015; Fan et al., 2016). Moreover, relationships between variables (called path coefficients) are standardized for effects of other variables and represent effect sizes, akin to partial regression coefficients. Path analysis is related but includes only empirically observed measurements (here called measures). Beyond path analysis, SEM also includes latent variables that represent conceptual constructs. For example, biodiversity is measured in many ways (e.g., species richness, abundances; Noss, 1990), and a latent variable called "biodiversity" can be represented by a linear statistical model of these measures. Critical for our purposes here, SEM enables statistical evaluation of relationships among latent variables, called paths (arrows in Fig. 2).

To test the alternative conservation hypotheses (Fig. 2) requires substantial data collected at each organizational level, among many well-defined systems. This requirement is rarely met in the literature because ecologists and conservation biologists naturally answer their specific questions by focusing on select systems, communities, or organisms. Here we use data collected in two very different wetland complexes on opposite US coasts, where biotic data represent vegetation. We chose these data sets because they represent large numbers of separate wetlands (N = 61 and 70), comparable to studying a total of 131 separate ecosystems. Results here may apply best to wetlands and inference may not extend directly to other systems, but results should at least bear implications for other systems. The systems differed in environmental disturbance context (urbanization vs. ranching) and details of data collection, which we considered a strength here because conclusions across different systems are more robust and general than if systems were groomed for similarity. Essentially, our use of two, separate study systems evaluates repeatability in different contexts.

Table 1

Measures for San Diego vernal pools and wetlands at Archbold Biological Station's Buck Island Ranch (BIR) in Florida. Two columns for BIR list alternative Ecosystem Functioning (EF) measures. See Appendix A for further details.

Latent variable	Measures		
	San Diego vernal pools EF = hydrology	BIR wetlands EF = hydrology	BIR wetlands EF = ranching
Species of Concern	No. listed basin species	No. conservative species	No. conservative species
	No. listed upland species	No. sensitive basin species	No. sensitive basin species
	No. endemic basin species	No. endemic species	No. endemic species
	No. endemic upland species	No. sensitive edge species	No. sensitive edge species
Community Diversity	Basin total species richness	Basin total species richness	Basin total species richness
	Upland total species richness	Edge total species richness	Edge total species richness
	Basin LCBD[a]	Basin LCBD	Basin LCBD
	Upland LCBD	Upland LCBD	Upland LCBD
Ecosystem Functioning	% cobbles & pebbles		Annual:perennial ratio
	Surface cracks (0–2 score)		Forb:graminoid ratio
	Mounds present? (0/1)		Forage quality
	Inlet modified? (0/1)		
	Outlet modified? (0/1)	Ditched? (0/1)	Percent woody species
	Intact soil (0–3 score)		Summer grazing intensity
	Sedimentation? (1–3 score)		Winter grazing intensity
	Maximum depth (cm)	Maximum depth (cm)	Average grazing intensity
	Catchment area (ha)	Volume (m^3)	No. months stocked/year
	Pool area (m^2)	Wetland area (ha)	
Landscape Integrity	Four 1-km quadrants integrity (1–6)	Area of wetlands within 400 m	Area of wetlands within 400 m
	Network basin integrities (0.2–1)	Ditch length within 400 m	Ditch length within 400 m
	Network catchment integrities (0.2–1)	Upland land use category (½)	Upland land use category (½)
	No. pools in complex	No. wetlands within 400 m radius	No. wetlands within 400 m radius
		Distance to road	Distance to road
		Water total P (mg/L)	Water total P (mg/L)
		Water conductivity	Water conductivity

[a] LCBD = local contribution to beta diversity (Legendre, 2014), which may be viewed as scoring a community's conservation value among similar regional communities.

2. Methods

2.1. Study systems

Vernal pools were once numerous in the San Diego area but most were obliterated during urban development (Bauder and MacMillan, 1998). Vernal pools vary in local geology and hydrology, ranging from isolated individual pools to complex surface flow networks. Hydroperiod depends on highly variable winter rain events; multi-annual dry intervals are not uncommon. Some remaining pools have been disturbed (e.g., soil disruption, flow modifications) in pool basins and/or catchments. Vernal pools of southern California include federally- and state-listed plant species, multiple plant endemics, and listed and endemic animals (Bauder, 2000; Simovich et al., 2013). Plant data were collected in 61 vernal pools in greater San Diego, California (Bauder et al., 2009). Ecosystem function (i.e., functional hydrology) and landscape integrity were measured directly and with indirect indicators, consistent with a rapid assessment protocol (see Bauder et al., 2009 and Bohonak and Bauder, 2011 for study system details). Indirect variables were statistically calibrated against direct measures of function collected over 20 years (Bohonak and Bauder, 2011) and used here because they correlate well with direct measures (Spearman rank correlation coefficients 0.67–0.88) and collected for more pools (Table 1).

We also studied seasonal, isolated wetlands in Florida on a ranch in the Everglades headwaters, where ~25% of land surface is wetlands (Swain et al., 2013). The depressional wetlands formed in the flat terrain from subsiding limestone bedrock. Typical hydroperiods are 6–9 months, with a summer-fall wet season and winter-spring dry interval. Buck Island Ranch is managed by Archbold Biological Station and includes > 600 wetlands on the 4170 ha property (Boughton et al., 2010). Wetlands are exposed to common ranchland practices including cattle grazing and prescribed fire and embedded in two pasture management intensities (highly managed and semi-natural). Highly managed pastures have been fertilized, ditched, disced, and seeded, and cattle graze in those pastures in summer. In contrast, semi-natural pastures have not been fertilized, were ditched less, never disced, and are grazed in winter when most plants are dormant. Pasture management intensity strongly affects vegetation; wetlands in highly managed pastures contain fewer native and more non-native plant species, and differ in functional groups from those in semi-natural pastures (see Boughton et al., 2010, 2011, 2016 for system details).

Seventy BIR wetlands were sampled (35 per pasture type) for plants, including endemics and species that are standard indicators of wetland quality (Cohen et al., 2004; Boughton et al., 2010). Ecosystem Functioning (EF) was evaluated as both hydrological and ranching variables (Table 1) because both matter in the regional context (Swain et al., 2013; Boughton et al., 2019) and we anticipated those two EFs would provide a separate test of conservation shortcuts related to ecosystem function for the BIR wetlands. As a result, 18 models were evaluated (6 for San Diego vernal pools, and 12 for Florida seasonal wetlands). Environmental, hydrological, and ranching-related variables were directly measured in all studied BIR wetlands (Table 1).
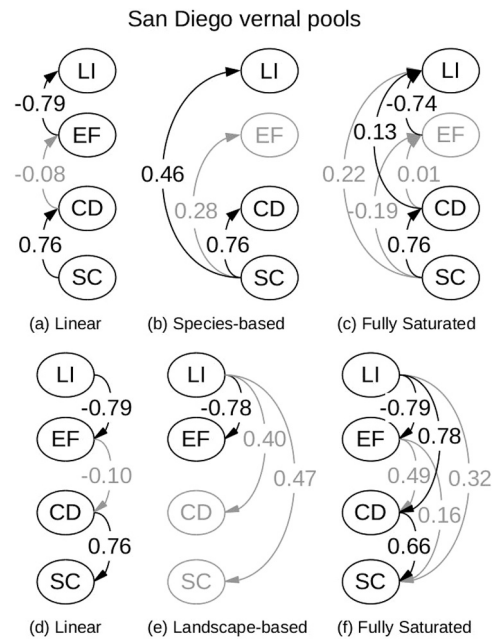
Fig. 3. Structural equation model results for San Diego vernal pools. Black latent variables (in ellipses) and path coefficients (numbers on arrows) were significant (10,000 bootstrap iterations); gray latent variables and path coefficients were not significant. Models are arrayed and latent variables are labeled as in Fig. 2. Also see Table 2 for model validation metrics and Appendix A for measurement variables used to reflect latent variables.

2.2. Structural equation models

We used partial least squares SEM (PLS-SEM) because it was more appropriate than covariance-based SEM (CB-SEM; Grace et al., 2000; Grace, 2006; Esposito Vinzi et al., 2010; Hair et al., 2011, 2013). The choice between the two methods depends on fundamental goals, practical matters of statistical distributions, and sample size (Haenlein and Kaplan, 2004; Reinartz et al., 2009; Esposito Vinzi et al., 2010; Hair et al., 2013; Jannoo et al., 2014; Stival dos Santos et al., 2015). Whereas CB-SEM is confirmatory for demonstrated theoretical models, PLS-SEM is designed for exploration, as was the case for indicator species and coarse-filter hypotheses here (Fig. 2). Also, CB-SEM maximizes variance among measures, whereas PLS-SEM maximizes variance explained by predictive relationships among LVs (our main interest here). Furthermore, measures here included a mixture of categorical and continuous variables, consistent with PLS-SEM but not with CB-SEM's assumption of multivariate normality. Finally, each study system included > 60 wetlands, which is relatively large for ecological studies but fewer than recommended for CB-SEM (Hair et al., 2006). With a statistical power of 0.80, > 60 systems and > 3 measures per LV, PLS-SEM models should detect significant ($p < 0.05$) coefficients of determination (R^2) as low as 0.25 (Hair et al., 2013). At least four measures were available for each LV (Table 1).

All measures were standardized (mean $= 0$, SD $= 1$) before model computation using the *semPLS* package in R (Monecke and Leisch, 2012). Equations matched Fig. 2 according to *semPLS* instructions. Latent variables were fitted to measures iteratively, where measures were removed if loadings (i.e., correlation coefficients) were < 0.2, and models were run again, as recommended by Götz et al. (2010). The 0.2 omission criterion here was more conservative than 0.4 recommended by Götz et al. (2010) because we compared nested models.

No single standard criterion exists to evaluate PLS-SEM fit; instead, each part of the model must be evaluated (Monecke and Leisch, 2012). We evaluated models using the following criteria, listed in decreasing order of importance:

1. Path coefficients (essentially partial regression coefficients, or effect sizes) between LVs and their significance, determined by bootstrapping with 1000 iterations.
2. Stone-Geisser Q^2 for assessment of predictive relevance per path coefficient. A preferred jackknife version of the coefficient of determination (R^2; Monecke and Leisch, 2012), where values < 0 indicate no predictive relevance and greater positive values indicate more relevance.
3. Significance of measure-LV relationships (loadings, or λ), determined by bootstrapping with 1000 iterations
4. Adjusted R^2 for a latent variable
5. Dillon-Goldstein's ρ, also referred to as composite reliability for the measures that reflect a LV, where ρ > 0.7 indicates a set of homogeneous measures.
6. Communality index, or the average R^2 between measures and their associated LVs
7. Redundancy index for endogenous LVs, or the portion of measure variability for an endogenous (downstream) LV that is explained by other, directly connected LVs.
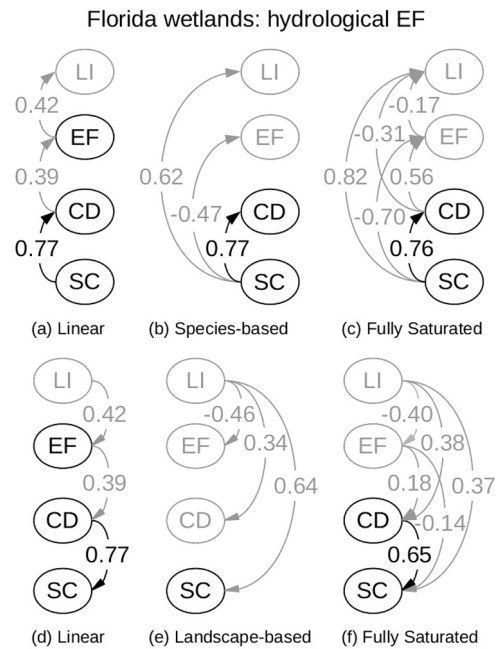
Fig. 4. Structural equation model results for ranch wetlands, using hydrological variables for Ecosystem Functioning (EF) and otherwise following Fig. 3.
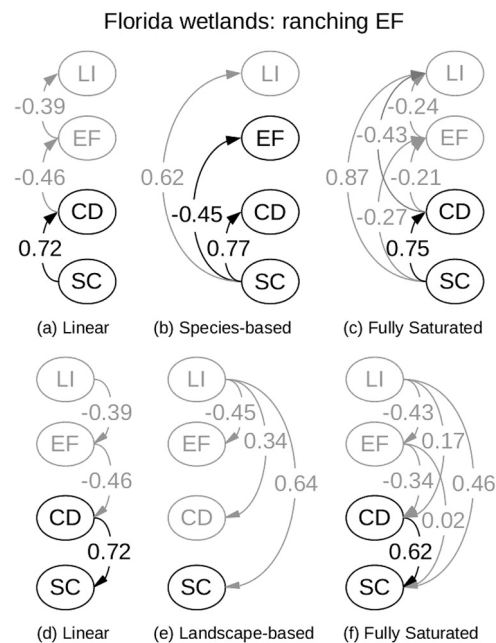
Fig. 5. Structural equation model results for ranch wetlands, using ranching variables for Ecosystem Functioning (EF) and otherwise following Fig. 3.

Criteria 1–3 were key to comparisons among models and data sets. Ideally, measures should significantly predict every LV and significant, predictive path coefficients should be obtained among those well-depicted LVs. Thus our criteria for minimal model success were:

a) all four LVs were significant,
b) at least one significant path coefficient predicting every endogenous LV,
c) a positive Q^2 value for each endogenous LV

Table 2

Model validation measures for models. Some measures (i.e., adjusted R^2, Q^2, redundancy) are not available for the exogenous (first) latent variable in a model. SC = Species of Concern, CD = Community Diversity, EF = Ecosystem Functioning, LI = Landscape Integrity. Florida wetlands (at BIR) were modeled twice; once for hydrological measures of Ecosystem Functioning, and for ranching-specific measures of Ecosystem Functioning. See Methods for explanation of model validation measures.

Study system	Model validation statistic	Latent variable	Indicator species approach			Coarse-filter approach		
			Linear	Species-based	Fully-saturated	Linear	Landscape-based	Fully-saturated
San Diego vernal pools	Q^2	SC	– –	– –	– –	0.29	0.06	0.20
		CD	0.21	0.21	0.21	-0.003	0.05	0.09
		EF	-0.004	-0.03	-0.03	0.26	0.26	0.22
		LI	0.30	0.05	0.34	– –	– –	– –
	Adjusted R^2	SC	– –	– –	– –	0.57	0.21	0.59
		CD	0.58	0.57	0.58	-0.01	0.15	0.22
		EF	-0.01	0.06	0.03	0.62	0.60	0.62
		LI	0.63	0.20	0.73	– –	– –	– –
	Dillon-Goldstein's ρ	SC	0.80	0.63	0.62	0.80	0.57	0.62
		CD	0.10	0.04	0.06	0.10	0.05	0.06
		EF	0.43	0.18	0.30	0.44	0.30	0.30
		LI	0.82	0.81	0.82	0.82	0.82	0.82
	Communality	SC	0.58	0.43	0.43	0.58	0.41	0.43
		CD	0.42	0.44	0.43	0.42	0.43	0.43
		EF	0.55	0.35	0.41	0.47	0.47	0.41
		LI	0.55	0.54	0.55	0.55	0.55	0.55
	Redundancy	SC	– –	– –	– –	0.34	0.09	0.26
		CD	0.25	0.25	0.25	0.004	0.07	0.11
		EF	0.004	0.03	0.01	0.29	0.29	0.26
		LI	0.35	0.11	0.40	– –	– –	– –
Florida wetlands hydrology	Q^2	SC	– –	– –	– –	0.39	0.24	0.50
		CD	0.23	0.23	0.22	0.02	-0.005	-0.05
		EF	< 0.001	0.01	0.002	-0.15	0.05	-0.07
		LI	0.02	0.08	0.05	– –	– –	– –
	Adjusted R^2	SC	– –	– –	– –	0.58	0.41	0.76
		CD	0.58	0.58	0.57	0.14	0.10	0.10
		EF	0.14	0.21	0.18	0.17	0.20	0.15
		LI	0.17	0.37	0.47	– –	– –	– –
	Dillon-Goldstein's ρ	SC	0.93	0.93	0.93	0.93	0.92	0.93
		CD	0.76	0.76	0.75	0.76	0.72	0.75
		EF	0.67	0.04	0.74	0.67	0.72	0.74
		LI	0.02	0.06	0.06	0.02	0.06	0.06
	Communality	SC	0.76	0.76	0.76	0.76	0.76	0.76
		CD	0.44	0.45	0.43	0.44	0.41	0.43
		EF	0.51	0.30	0.43	0.51	0.58	0.43
		LI	0.38	0.35	0.34	0.38	0.34	0.34
	Redundancy	SC	– –	– –	– –	0.44	0.31	0.58
		CD	0.26	0.26	0.25	0.07	0.05	0.05
		EF	0.08	0.06	0.09	0.09	0.12	0.07
		LI	0.07	0.13	0.17	– –	– –	– –
Florida wetlands ranching	Q^2	SC	– –	– –	– –	0.32	0.21	0.51
		CD	0.21	0.23	0.20	0.05	-0.01	0.01
		EF	0.06	0.04	0.03	0.02	0.01	0.03
		LI	0.01	0.08	0.12	– –	– –	– –
	Adjusted R^2	SC	– –	– –	– –	0.52	0.40	0.74
		CD	0.52	0.58	0.56	0.20	0.10	0.17
		EF	0.20	0.19	0.17	0.14	0.19	0.17
		LI	0.14	0.37	0.50	– –	– –	– –
	Dillon-Goldstein's ρ	SC	0.92	0.93	0.93	0.92	0.92	0.93
		CD	0.75	0.76	0.76	0.75	0.70	0.76
		EF	0.69	0.58	0.63	0.69	0.56	0.63
		LI	0.01	0.06	0.05	0.01	0.04	0.05
	Communality	SC	0.75	0.76	0.76	0.75	0.75	0.76
		CD	0.47	0.45	0.46	0.47	0.40	0.46
		EF	0.43	0.32	0.34	0.43	0.26	0.34
		LI	0.37	0.35	0.33	0.37	0.35	0.33
	Redundancy	SC	– –	– –	– –	0.39	0.31	0.57
		CD	0.24	0.26	0.26	0.10	0.04	0.09
		EF	0.09	0.06	0.07	0.06	0.05	0.06
		LI	0.06	0.13	0.17	– –	– –	– –

Table 3
Most successful paths were between Species of Concern and Community Diversity, which were themselves more often significantly indicated by measurement variables than were Ecosystem Functioning and Landscape Integrity (see Appendices for details). The table is a matrix, where bold values on the diagonal are the percentage of models (of 18 total) for which that latent variable (LV) was significant. Values above the diagonal are the fractions of successful paths for indicator species models. Values below the diagonal are the fractions of successful paths for coarse-filter models. Success was indicated by a significant path coefficient between two significant LVs.

	Species of concern	Community diversity	Ecosystem functioning	Landscape integrity
Species of concern	**94%**	9/9	1/6	1/6
Community diversity	6/6	**83%**	0/6	1/3
Ecosystem functioning	0/3	0/6	**39%**	2/6
Landscape integrity	0/6	1/6	3/9	**33%**

Beyond those minima, the most predictive models include LVs with Q^2 values > 0.50, $\rho > 0.7$, high communalities, and low redundancies. By these criteria, model failure is indicated if LVs were not significant, endogenous LVs were not predicted by significant path coefficients, and low or negative Q^2 values were obtained.

3. Results

Results are summarized graphically (Figs. 3–5) to replicate the SEM-based hypotheses (Fig. 2) and depict significant ($\alpha = 0.05$) LVs and path coefficients in black and nonsignificant terms in gray. For visual clarity, other model metrics are reported in Table 2, and measures and their significance values are listed in Appendix A.

3.1. San Diego vernal pools

Biotic subsets of models (i.e., SC-CD in Fig. 3, except Fig. 3e) met minimal criteria for success by having statistically significant LVs and path coefficients, as well as positive Q^2 values. However, Q^2 values did not exceed 0.21; Table 2, meaning the biotic approach had limited predictive relevance.

No indicator species model for vernal pools met minimum criteria for success (Fig. 3a–c). Ecosystem Functioning (EF) was not significantly predicted by measurement variables in two models, and in all indicator species models EF could not be significantly predicted by SC or CD and lacked predictive relevance (all $Q^2 < 0$; Table 2). Overall, indicator species models had weak predictive relevance (no Q^2 exceeded 0.35), although EF-LI and SC-CD path coefficients were strong and statistically significant (Fig. 3a–c).

Coarse-filter models also struggled to span more than two hierarchical levels (Fig. 3d–f). The linear model could not predict through all four organizational levels, and the landscape-based model did not significantly predict CD and SC. Only the fully saturated model met minimal criteria for success, with statistically significant LVs linked by at least one significant path coefficient and positive Q^2 values (Fig. 3f, Table 2). However, all Q^2 values were relatively low (< 0.2) in the fully saturated model, especially CD (Table 2). Thus, even the fully-saturated model could only weakly predict the LI-EF, LI-CD, and CD-SC paths.

3.2. Florida wetlands; hydrology

The biotic approach was consistently supported within the indicator species models, though with modest and variable predictive relevance (Table 2). Neither indicator species nor coarse filter models met minimal criteria for success. At least one LV was not significant in every model, only path coefficients between SC and CD were significant (Fig. 4), and the maximal Q^2 was 0.50 (Table 2). We note that SC was always significant, CD was significant in 4 of 6 models, and EF was significant in two models. Though LI was never significantly represented by measures, the same conclusion would be obtained if models had not included LI. In sum, no support for indicator species or coarse-filter approaches was obtained for this data set.

3.3. Florida wetlands; ranching

As before, SC and CD were inter-predictive (Table 2), supporting a biotic approach. But the indicator species and coarse-filter models failed again to meet minimal success criteria. No indicator species and coarse-filter model included four significant LVs, and path coefficients across mid-level LVs were not significant (Fig. 5). Predictive relevance (Q^2) values were quite low for LI and EF, and ranged between 0.2 and 0.5 for SC and CD (Table 2). Other model validation measures were satisfactory, including some strong ρ and communality values and low redundancy (Table 2). We concluded that the biotic approach was again supported and that difficulty finding conservation shortcuts in Florida wetlands models were not due to the use of hydrological EF estimates.

3.4. Summary

General patterns for shortcuts among models can be summarized (Table 3) using criteria for success applied uniformly among all models (i.e., connect two significant LVs with a significant path coefficient). Among all models, most potential paths were to the next organizational level (N = 42); potential shortcuts that skipped one (N = 18) or two organizational levels (N = 12) were less possible. Thus for fair comparisons, we consider successful shortcuts relative to the number possible.

Both SC and CD were often significantly related to their respective measures (Appendix A). In turn, paths between those LVs (called biotic shortcuts here) were always successful, where modeled (Table 3). But LVs at greater organizational levels (EF, LI) were less often significantly related to their respective measures. Accordingly, few paths between biotic LVs (SC, CD) and EF or LI were successful. Also, a minority of paths between EF and LI were successful.

4. Discussion

Conservation strategies for particular goals are often assumed to offer shortcuts to other conservation goals. We found little support (1 of 18 cases, or 5%, and that one case was not highly predictive) for either indicator species or coarse-filter conservation shortcuts in two study systems. In contrast, the more limited biotic approach was repeatedly supported.

The indicator species approach assumes that conservation of select indicator species predictably protects greater ecological organization levels (communities, ecosystems, landscapes). Conversely, the coarse-filter approach targets conservation to entire landscapes or ecosystems, with the assumption lesser ecological organization levels may also be protected. The systems used to evaluate conservation shortcuts here were well studied, contain multiple species of concern, and exist as numerous, discretely-bounded units. We do not pretend that results here must generalize, but we do think the opportunity to evaluate the hypotheses afforded by the two systems is relatively rare elsewhere. Results here indicate caution in assuming these conservation shortcuts, especially in systems that may be less replicated, less clearly defined, and less quantified than systems studied here.

Conservation biologists may expect that indicator species and coarse filter approaches are complementary and should be applied in tandem (Jenkins, 1985). If so, then both conservation approaches should have been statistically supported within each study system; this was not the case. Instead, results lead us to agree with others who have concluded that coarse-filter and indicator species approaches are insufficient (Noss, 1990, 1996; Andelman and Fagan, 2000; Araújo et al., 2001; Segura et al., 2014; Grantham et al., 2010; Januchowski-Hartley et al., 2011; Hermoso et al., 2013). We emphasize that species-, community-, ecosystem-, or landscape-centric conservation strategies are not the problem; instead, the problem arises when a conservation strategy is assumed to provide conservation benefits for another organizational level (i.e., a shortcut). Assumed shortcuts could harm conservation efforts rather than help meet goals if shortcuts are ineffective. For example, protection of entire vernal pool complexes, by itself, should not be expected to be sufficient to conserve community diversity and species of concern in San Diego vernal pools. Active management within organizational levels should also be expected rather than assumed benefits across levels, including clear performance standards relative to reference sites, long-term monitoring, and separate management of plant and animal diversity (Schlatter et al., 2016).

The hypotheses tested here may also be evaluated with SEMs for other systems. If our general conclusions are repeatable, conservation planning should not typically expect shortcuts. Instead, efforts aimed to a certain goal (e.g., protection of an endangered species) must be supplemented by other efforts targeted appropriately to other organizational levels (Tingley et al., 2014). To be clear, it remains possible that conservation efforts aimed to species of concern may benefit ecosystems and landscapes (Lyons et al., 2005), but our results suggest it is unlikely or slow. For example, re-introduced gray wolves in the Greater Yellowstone Ecosystem are a potential driver of recovery for riparian woody vegetation and river structure (due to beaver ponds), thus affecting ecological functioning and landscape integrity (Wolf et al., 2007; Kauffman et al., 2010; Ripple et al., 2015). However, those effects require decades and/or active management of multiple other system components (e.g., beavers, bison, etc.; Smith and Tyers, 2012; Beschta and Ripple, 2012, 2015, 2019). Thus, even in the well-studied case of the Greater Yellowstone Ecosystem with a strong trophic cascade via wolves, a conservation shortcut appears slow to serve as an exception proving the rule.

Assume for a moment that our results do indicate a rule. If so, then conservation planning should have the same default, skeptical (i.e., scientific) expectation that other disciplines of complex systems have also concluded – that shortcuts do not exist (Hydén, 1983; Berry, 2001; Brevini et al., 2010; Campbell, 2013). Accordingly, we recommend that "fine-filter" efforts to conserve species of concern be allowed to focus on that worthy goal, without heaping on great expectations that ecosystem function or landscape integrity necessarily follow. Likewise, "coarse-filter" efforts planned to conserve landscapes or ecosystems should maintain focus on those valuable outcomes, and should not assume by default that benefits convey to communities or species of concern.

Given that cautious tone regarding conservation shortcuts, it is encouraging that biotic shortcuts (i.e., between species of concern and community diversity) were typically supported and perhaps predictive (mean predictive relevance (Q^2) = 0.26, whereas Q^2 > 0.50 indicates a predictive model; Chin, 2010). Weak autocorrelation may exist between SC and CD because Species of Concern contribute to community diversity, but those species were infrequently recorded and not often abundant (thus their status). Results here support cross-taxon approaches within the same habitats, though this should not necessarily be assumed (Rodrigues and Brooks, 2007; Wiens et al., 2008). We note that ecosystem engineers, flagship/umbrella/keystone species, and strongly interactive species (Soulé et al., 2003) were not considered here, though multiple species were federally-listed endangered species (Bauder et al., 2009) or standard indicators of wetland quality (Boughton et al., 2010, 2016). We expect that focused efforts to attain greater predictive relevance for biotic approaches could be successful in both study systems, and perhaps for other systems. More generally, prior work on biotic shortcuts (e.g., Lambeck, 1997; Simberloff, 1998; Andelman and Fagan, 2000; Ficken et al., 2019; Ficken and Rooney, 2020) appears warranted and potentially more fruitful than continued searches for shortcuts spanning more organizational levels.

What arguments may counter our interpretation? Several come to mind, along with our counter-arguments. Perhaps the studies were conducted at inappropriate spatial scales or used the wrong measures. This potential concern exists for any study that finds weak effects,but is countered here by the fact that study systems encompassed local and regional spatial scales for the study organisms (i.e., not driving distances), with more study units than most other studies and data collected by multiple disciplines. We suggest that the study systems offer a strong test of indicator-species and coarse-filter approaches in conservation.

Perhaps historical biogeography shaped species distributions rather than relatively recent ecosystem and landscape conditions (Hermoso et al., 2013; Araujo et al., 2001; Januchowski-Hartley et al., 2011). This biogeographical argument may apply best to study areas with much greater spatial extent than studied here, and for select taxa. Also, many organisms counter historical effects at local scales by shifting contemporary abundance and distribution in response to recent or current environmental conditions, consistent with the Grinnellian niche concept, metacommunity theory, and the standard practices of biological monitoring for anthropogenic pollutants and wetland classification (Karr and Chu, 1998; Tiner, 1999; Leibold et al., 2004; Vázquez-Rivera and Currie, 2015).

Perhaps the opposite argument applies: current conditions affected species' spatial distributions but sampling or measured variables recorded here missed those existing effects. We offer four counterarguments. Foremost, relationships *among constructs* (i.e., latent variables) emphasized here were the point of analyses and often found lacking. Measurements of constructs were less often the problem; most constructs (46 of 72, or 64% of construct events) were significantly represented by measured variables. Also, sampling was fully sufficient to record multiple rare species in both study systems (Bauder et al., 2009; Boughton et al., 2010, 2016), and the number of separate units within each study system (61 in San Diego, 70 in Florida) was large compared to most ecological studies, with sufficient power to detect potential effects. Third, the study systems were data-rich at all four organizational levels with significant relationships between environmental conditions and biota (Bauder, 2000; Boughton et al., 2010, 2016). Finally, weak relationships between hydrological (and ranching-related) EF and CD or SC occurred despite collaborations with professional hydrologists in both systems (i.e., naïve ecologists did not work alone here in these relatively large study systems).

Finally, some may wonder if SEM is the right tool for the job. A long list of peer-reviewed SEM research demonstrates this analytical approach is fully appropriate because it sensitively evaluates multicausal systems as hypothesized here (e.g., Grace et al., 2000, 2012, 2016; Seabloom et al., 2006; Grace, 2006; Harrison et al., 2006; Hermoso et al., 2013; Stival dos Santos et al., 2015; Fan et al., 2016; Sha et al., 2017). If anything, partial least squares SEM used here is more appropriate than the many cases of SEMs in ecology, for reasons summarized in Section 2.1 above.

In summary, species of concern often predicted community diversity (and vice versa), but shortcuts between more distant organizational levels were hard to find. The two study systems were highly replicated, and composed of discrete, relatively small, and thus well-described populations, communities, and ecosystems that were embedded in multiple landscapes. We expect that effective shortcuts will be difficult to empirically demonstrate for many other systems that do not share all those attributes. Instead, regional ensemble conservation goals and approaches will be more often effective than assumed conservation shortcuts.

A coarse filter approach is increasingly justified given rapid climate change and unpredictable species distributions (Hunter et al., 1988; Beier et al., 2015; Lawler et al., 2015). But species of concern also require active conservation. Like other disciplines, we suggest that conservation biology should move beyond its quest for big shortcuts (Hydén, 1983; Simberloff, 1998; Morrison et al., 1998; Smallwood, 2000; Berry, 2001; Heino et al., 2005; Brevini et al., 2010; Campbell, 2013). Instead, an ensemble of conservation approaches within and among regions may be most valuable (Tingley et al., 2010). We recommend that conservation biology:

a) empirically evaluate potential shortcuts using approaches like that used here
b) expect by default that a good shortcut will be hard to find (i.e., be skeptical)
c) emphasize ensemble conservation goals and approaches in a region (Tingley et al. 2014)
d) apply more sophisticated and predictive approaches to conservation planning (e.g., Albuquerque and Beier, 2015)
e) consider how those approaches may adapt in the Anthropocene (Ellis, 2015).

Results here indicate the best shortcuts will be short ones, along paths within and among species of concern and community diversity. Continued investigation and use of these biotic shortcuts appears to be better justified than continued searches for long-range shortcuts.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix A. Measurement variable details and coefficients for model results depicted in Figs. 3–5. All variables were standardized to mean = 0 and SD = 1 before SEM

San Diego Vernal Pools
Variable definitions from Bauder et al. (2009) unless otherwise listed.
Species of Concern

1. Number of plant species in a pool basin that are listed as endangered, threatened or rare by California or the U.S. Based on Category 1 plants
2. Number of plant species in the immediately surrounding upland that are listed as endangered, threatened or rare by California or the U.S. Based on Category 1 plants
3. Number of upland plant species in a pool basin that are endemics. Based on Category 2 plants
4. Number of basin plant species in the immediately surrounding upland that are endemics. Based on Category 2 plants
   Community Diversity

5. Vegetation species richness in the basin
6. Vegetation species richness in the immediately surrounding upland
7. Vegetation Local Contribution to Beta Diversity, basin (LCBD; Legendre, P, Cáceres, M. 2013. Beta diversity as the variance of community data: dissimilarity coefficients and partitioning. Ecology Letters 16:951–963).
8. Vegetation LCBD, upland
   Ecosystem Functioning (related to Surface and Subsurface Water Storage)
9. Cobbles and pebbles as a percent of the basin covered. Pebbles are 2–7.5 cm in diameter and cobbles are 7.5–25 cm in diameter
10. Surface cracks. 0 = no, 1 = shallow, 2 = deep, where deep is > 1 cm wide & 1 dm deep
11. Presence or absence (1/0) of mounds in the basin (a feature of natural basins)
12. Inlet modification: 0 = none, 1 = raised, lowered, or trenched/ditched.
13. Outlet modification: 0 = none, 1 = raised, lowered, or trenched/ditched.
14. Intact soil: 1 = severe disruption, 2 = moderate, 3 = more intact.
15. Sedimentation: deltaic deposition or soil discontinuities. 0 = none, 1 = present.
16. Pool maximum depth (m)
17. Catchment area of a pool (ha)
18. Pool area (m^2)
   Landscape Integrity
19. Integrity of four 1-km quadrants around each basin (range = 1–6)
20. Integrity of basins in the network (range = 1–6)
21. Integrity of network catchment area (range = 1–6)
22. Number of pools in complex

(See Tables A1–A6).
Florida Seasonal Wetlands (At Buck Island Ranch)
Species of Concern

1. No. Endemic species
2. No. Conservative species (species that have a CC score of 7 or greater)
3. No. Sensitive species (significant indicators of SN wetlands) in center zone
4. No. Sensitive species in edge zone
   Community Diversity
5. Total center species richness
6. Total edge species richness
7. Total center Local Contribution to Beta Diversity (LCBD; Legendre)
8. Total edge LCBD
   Ecosystem Functioning – Hydrological variables 9–12, Ranching variables 13–20
9. Maximum depth (cm)
10. Wetland area (ha)
11. Ditched? (0/1)
12. volume (m^3)
13. Annual: Perennial Ratio
14. Forb: Graminoid Ratio
15. Forage quality (percent palatable plants)
16. Percent woody species
17. Summer, April 1 - Aug 31. the number of cows * number of days in the pasture (added for each event), divided by acreage of the pasture, divided by the number of days in the season (153 days for summer)
18. Winter, Sept 1-March 31. Same calculation as above, but divided by 212 days for winter
19. Average of winter and summer
20. Number of days stocked per year (~disturbance extent)
   Landscape Integrity
21. Number of wetlands within 400 m
22. Area of wetlands within 400 m
23. Length of ditches within 400 m
24. Upland land use (intensively-managed or semi-natural)
25. Distance to road (m)
26. Total P (mg/L) – related to pasture modifications by fertilizer application
27. Conductivity (μS/cm) – related to pasture modifications by lime application

Table A1

Measurement variable coefficients (λ) for indicator species models of San Diego vernal pools. Measurement variable numbers match list above. Coefficients that are missing (- -) were < 0.20 and excluded in preliminary analyses. Significance (Sig.) asterisks indicate p < 0.05, based on 95% confidence intervals (CIs) that did not include zero.

Measure	Linear		Species-based		Fully saturated	
	Coefficient	Sig.	Coefficient	Sig.	Coefficient	Sig.
1	0.56	*	0.53	*	0.51	*
2	− −		− 0.21		− 0.23	
3	0.82	*	0.76	*	0.76	*
4	0.87	*	0.89	*	0.90	*
5	0.75	*	0.70	*	0.73	*
6	0.77	*	0.75	*	0.75	*
7	− 0.58	*	− 0.64	*	− 0.64	*
8	− 0.43		− 0.53	*	− 0.45	
9	− 0.47	*	0.48		− 0.43	*
10	− −		0.39		− 0.26	
11	− −		− −		− −	
12	0.78	*	− 0.65		0.77	*
13	0.87	*	− 0.74		0.85	*
14	− 0.90	*	0.83		− 0.91	*
15	0.89	*	− 0.76		0.86	*
16	0.28		− 0.39		0.31	
17	− −		− 0.24		0.23	
18	− −		− −		− −	
19	0.62	*	0.43		0.48	*
20	0.94	*	0.90	*	0.92	*
21	0.85	*	0.93	*	0.91	*
22	0.47	*	0.56	*	0.54	*

Table A2

Measurement variable coefficients (λ) for coarse-filter models of San Diego vernal pools. Measurement variable numbers match list above. Coefficients that are missing (- -) were < 0.20 and excluded in preliminary analyses. Significance (Sig.) asterisks indicate p < 0.05, based on 95% confidence intervals (CIs) that did not include zero.

Measure	Linear		Landscape-based		Fully saturated	
	Coefficient	Sig.	Coefficient	Sig.	Coefficient	Sig.
1	0.57	*	0.47		0.51	*
2	− −		− 0.32		− 0.23	
3	0.82	*	0.72		0.76	*
4	0.87	*	0.90		0.90	*
5	0.76	*	0.73		0.73	*
6	0.76	*	0.72		0.75	*
7	− 0.59	*	− 0.68		− 0.64	*
8	− 0.44		− 0.43		− 0.45	
9	− 0.49	*	− 0.42	*	− 0.43	*
10	− −		− 0.23		− 0.26	
11	− −		− −		− −	
12	0.76	*	0.78	*	0.77	*
13	0.84	*	0.89	*	0.84	*
14	− 0.90	*	− 0.91	*	− 0.91	*
15	0.86	*	0.90	*	0.86	*
16	0.34		0.23		0.31	
17	0.28		− −		0.23	
18	− −		− −		− −	
19	0.62	*	0.49	*	0.48	*
20	0.94	*	0.92	*	0.92	*
21	0.85	*	0.91	*	0.91	*
22	0.45	*	0.54	*	0.54	*

Table A3

Measurement variable coefficients (λ) for indicator species models of Florida (Buck Island Ranch) wetlands, using hydrological measures of Ecosystem Functioning. Measurement variable numbers match list above. Coefficients that are missing (- -) were < 0.20 and excluded in preliminary analyses. Significance (Sig.) asterisks indicate p < 0.05, based on 95% confidence intervals (CIs) that did not include zero.

Measure	Linear		Species-based		Fully saturated	
	Coefficient	Sig.	Coefficient	Sig.	Coefficient	Sig.
1	0.91	*	0.90	*	0.91	*
2	0.90	*	0.89	*	0.88	*
3	0.73	*	0.76	*	0.75	*
4	0.93	*	0.93	*	0.93	*
5	0.54	*	0.49	*	0.62	*
6	0.78		0.80	*	0.83	*
7	0.61	*	0.62	*	0.51	
8	0.71	*	0.72	*	0.63	
9	0.61	*	− 0.24		0.72	
10	0.88	*	− 0.47		0.53	
11	− 0.37		0.83		0.82	
12	0.88	*	− 0.46		0.51	
21	− −		0.50		0.46	
22	0.90		0.64		0.65	
23	− 0.66		− 0.83		− 0.83	
24	0.65		0.83		0.81	
25	− −		0.23		0.28	
26	− 0.31		− 0.35		− 0.35	
27	− 0.34		− 0.49		− 0.47	

Table A4

Measurement variable coefficients (λ) for coarse-filter models of Florida (Buck Island Ranch) wetlands, using hydrological measures of Ecosystem Functioning. Measurement variable numbers match list above. Coefficients that are missing (- -) were < 0.20 and excluded in preliminary analyses. Significance (Sig.) asterisks indicate p < 0.05, based on 95% confidence intervals (CIs) that did not include zero.

Measure	Linear		Landscape-based		Fully saturated	
	Coefficient	Sig.	Coefficient	Sig.	Coefficient	Sig.
1	0.91	*	0.89	*	0.91	*
2	0.90	*	0.86	*	0.88	*
3	0.73	*	0.80	*	0.75	*
4	0.93	*	0.93	*	0.93	*
5	0.54	*	0.69		0.62	*
6	0.78	*	0.87		0.83	*
7	0.61		0.35		0.51	
8	0.71	*	0.54		0.63	
9	0.61	*	0.54		0.72	
10	0.88	*	− −		0.53	
11	− 0.37		0.94		0.82	
12	0.88	*	− −		0.51	
21	− −		0.47		0.46	
22	0.90		0.66		0.65	
23	− 0.66		− 0.82		− 0.83	
24	0.65		0.81		0.81	
25	− −		0.26		0.28	
26	− 0.31		− 0.36		− 0.35	
27	− 0.34		− 0.48		− 0.47	

Table A5

Measurement variable coefficients (λ) for indicator species models of Florida (Buck Island Ranch) wetlands, using ranching measures of Ecosystem Functioning. Measurement variable numbers match list above. Coefficients that are missing (- -) were < 0.20 and excluded in preliminary analyses. Significance (Sig.) asterisks indicate p < 0.05, based on 95% confidence intervals (CIs) that did not include zero.

Measure	Linear		Species-based		Fully saturated	
	Coefficient	Sig.	Coefficient	Sig.	Coefficient	Sig.
1	0.92	*	0.91	*	0.91	*
2	0.91	*	0.89	*	0.89	*
3	0.70	*	0.75	*	0.74	*
4	0.92	*	0.93	*	0.93	*
5	0.22		0.49	*	0.35	
6	0.62	*	0.80	*	0.72	*
7	0.82	*	0.62	*	0.72	
8	0.87	*	0.72	*	0.82	
13	– –		0.37		0.29	
14	– –		– –		– –	
15	– –		– –		– –	
16	− 0.28		− 0.32		− 0.28	
17	0.81		0.87	*	0.84	
18	0.54		0.33		0.44	
19	0.96		0.87	*	0.93	
20	0.46		0.26		0.37	
21	0.34		0.50		0.39	
22	0.73		0.64		0.69	
23	− 0.77		− 0.83		− 0.81	
24	0.79		0.83		0.80	
25	– –		0.23		0.25	
26	− 0.45		− 0.35		− 0.39	
27	− 0.43		− 0.49		− 0.46	

Table A6

Measurement variable coefficients (λ) for coarse-filter models of Florida (Buck Island Ranch) wetlands, using ranching measures of Ecosystem Functioning. Measurement variable numbers match list above. Coefficients that are missing (- -) were < 0.20 and excluded in preliminary analyses. Significance (Sig.) asterisks indicate p < 0.05, based on 95% confidence intervals (CIs) that did not include zero.

Measure	Linear		Landscape-based		Fully saturated	
	Coefficient	Sig.	Coefficient	Sig.	Coefficient	Sig.
1	0.92	*	0.89	*	0.909	*
2	0.91	*	0.86	*	0.889	*
3	0.70	*	0.80	*	0.742	*
4	0.92	*	0.93	*	0.929	*
5	0.22		0.73		0.354	
6	0.62	*	0.87		0.721	*
7	0.82	*	0.29		0.72	
8	0.87	*	0.48		0.815	
13	– –		0.52		0.286	
14	– –		0.26		– –	
15	– –		− 0.28		– –	
16	− 0.28		− 0.13		− 0.285	
17	0.81		0.79		0.843	
18	0.53		0.42		0.441	
19	0.96		0.87		0.925	
20	0.46		0.28		0.367	
21	0.34		0.46		0.387	
22	0.73		0.65		0.688	
23	− 0.77		− 0.80		− 0.806	
24	0.79		0.81		0.8	
25	– –		0.23		0.253	
26	− 0.45		− 0.42		− 0.386	
27	− 0.43		− 0.51		− 0.456	

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