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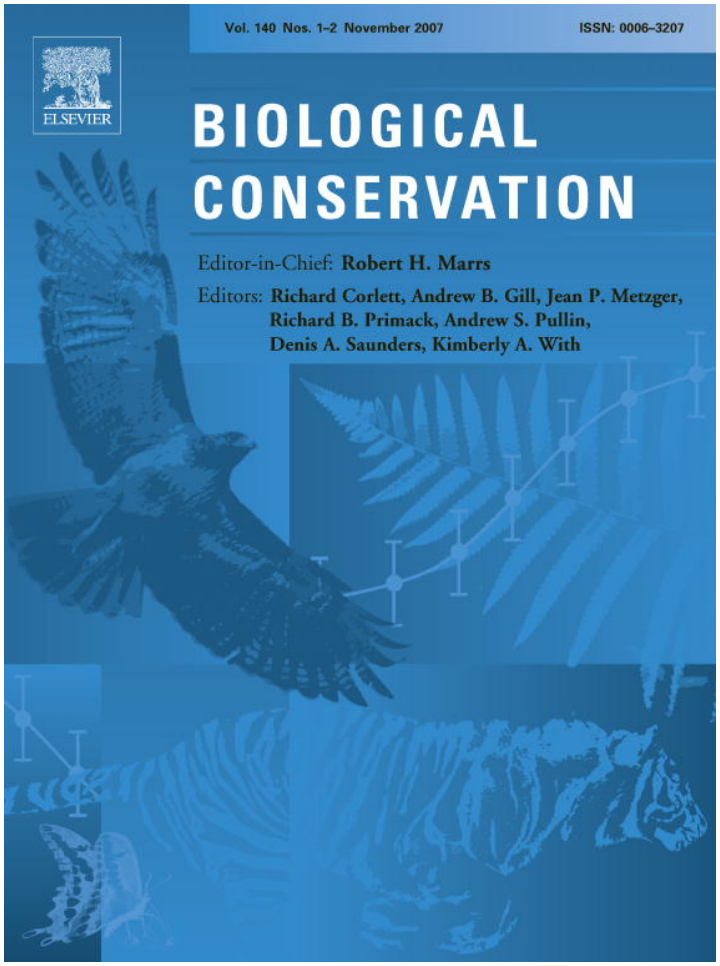

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Developing terrestrial, multi-taxon indices of biological integrity: An example from coastal sage scrub

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ABSTRACT

We screened 351 species or genera for their response to disturbance in coastal sage scrub (CSS) to develop a 15-metric, 5-taxon Index of Biological Integrity (IBI). We collected data on ants, birds, herpetofauna, small mammals, and plants for two years on 46 sites established across a gradient of disturbance in three reserves. The gradient spanned relatively intact CSS with thick stands of shrubs, to former CSS stands type-converted to exotic grasses. ANOVAs and clustering analyses indicated the IBI could distinguish four levels of disturbance in CSS. General measures of community structure, such as richness, did not show changes across the gradient for most taxa, and responses of taxa across the gradient were varied and rarely correlated. However, turnover in species or genera across the gradient was common across all taxa as shrub-obligate life forms were replaced by those favoring grassy or disturbed habitats. Our data indicate index-based approaches based on data collected across disturbance gradients may outperform more traditional community level metrics when responses to anthropogenic influences are complex and vary across species.
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1. Introduction

Early definitions of biological integrity emerged from an Environmental Protection Agency symposium held in 1975 (Ballentine and Guarraia, 1977). Currently, the most commonly used definition of biological integrity is that proposed by Karr and Dudley (1981): "the capability of supporting and maintaining a balanced, integrated, adaptive community of organisms having a species composition, diversity and functional organization comparable to that of natural habitats in the region". The Index of Biological Integrity (IBI) was proposed by Karr (1981) as a relative measure of biological integrity while Karr and Chu (1999) described protocols for IBI development. IBIs are unique indices because they: (1) are developed from data collected across a specified anthropogenic disturbance gradient where undisturbed sites are considered references for high biological integrity; (2) use patterns of change from the reference conditions to develop and select metrics; and (3) combine information from multiple metrics into a single value (Karr and Chu, 1999).

Indices are often based on a wide range of community level metrics (species richness, Shannon-Weiner diversity, etc.). In some cases, such as in plant based indices, *a priori* designations or weighting regimes are used to convert a diversity index into a metric with conservation utility (Taft et al., 2006). By contrast, a community level metric would only be used in an IBI if it responded across the disturbance gradient, and it would be combined with a suite of other metrics.

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Further, IBIs, as defined by Karr and Chu (1999), do not use *a priori* ranking regimes because the metrics in the IBI are derived from the data collected.

The IBI is widely used to monitor streams and rivers in the USA, Canada, and Europe (Pont et al., 2006) and has lead to changes in assessment under the Clean Water Act in the USA (Davis et al., 1996). In contrast, terrestrial ecologists are just beginning to develop IBIs and few, if any, are used by regulatory agencies. Specific taxa have been studied as terrestrial bioindicators (Kremen et al., 1993; Borges et al., 2000; Hess et al., 2006; Taft et al., 2006; Pohl et al., 2007), and a small number of IBIs or IBI-related measures have been developed including those for shrub-steppe habitats (Karr and Chu, 1999; Kimberling et al., 2001), rangelands and grasslands (Bradford et al., 1998; Borges et al., 2000; Browder et al., 2002; Taft et al., 2006), and forests (Brooks et al., 1996; Majer and Beeston, 1996; Brooks et al., 1998; O'Connell et al., 2000; Glennon and Porter, 2005; Cardoso et al., 2006).

The vast majority of IBIs are based on data from just one taxon, despite calls for more integrative approaches (Karr, 1993; Andreasen et al., 2001; Niemi et al., 2004). Multi-taxon IBIs should provide a more integrative measure of system response to disturbance and perhaps increase an indicator's sensitivity (Niemi et al., 2004). Despite this, few multi-taxon IBIs exist. Croonquist and Brooks (1991) analysed data from small mammals and birds collected at the same locations but did not integrate these into a single indicator. However, in the only example we found, Brooks et al. (1998) provide a detailed illustration of how a multi-taxon IBI could be developed.

Here we describe the development of a multi-taxon IBI for coastal sage scrub (CSS). CSS is a shrub-dominated community in southern California, supporting many endangered and threatened species. Urbanization has resulted in ~85% loss of CSS area (O'Leary, 1995). Efforts to conserve remaining CSS include new Habitat Conservation Plans (HCPs) (Holling, 1997; Babbit, 1999; Pollak, 2001). HCPs are legally required to develop large-scale monitoring programs, though few have done so (USFWS and NMFS, 1996; Greer, 2004).

Perhaps the greatest threat to CSS is increased fire frequency. CSS is a fire adapted plant community with an historical fire regime of scattered small fires and rare wind driven fires that burn large areas (Keeley and Fotheringham, 2001). As human populations grow in southern California so do fire ignitions, and fire frequency has increased from ~100 fires per decade to ~500 (Keeley and Fotheringham, 2001). Frequent fires favor exotic grasses over native shrubs, which can result in a positive feedback loop between exotic grass invasion and shorter fire return intervals (D'Antonio and Vitousek, 1992; Brooks et al., 2004) ultimately converting CSS into exotic grasslands (Keeley, 1990; Minnich and Dezzani, 1998; Keeley, 2001).

Cost-effective monitoring in CSS is crucial for effective management (Atkinson et al., 2004) and researchers investigating the potential of indicator species have found little support. Chase et al. (2000) concluded 14 species of conservation concern could not be used as indicators of richness and none of the 37 species evaluated were strong predictors of diversity hotspots. In addition, two studies of California Gnatcatchers, a key species in CSS conservation, indicated they did not function as surrogates for diversity in other taxonomic groups (Chase et al., 1998; Rubinoff, 2001). However, Case and Fisher (2001) identified four lizard species that were correlated with herpetofauna-rich locations. This failure of indicators is likely caused by the wide variation of observed responses to anthropogenic disturbance (Guthrie, 1974; Lovio, 1996; Bolger et al., 1997; Chase et al., 2000; Crooks et al., 2004).

Given the poor success of single species approaches and the wide variety of responses to disturbance observed in previous studies, we felt a multi-taxon IBI could be an effective measure of relative biological integrity in CSS. In addition, given the role of fire in the expansion of exotic grasses, we felt developing the IBI across a gradient of exotic invasion would increase its utility to managers. Thus, the goals of our work were to: (1) develop a multi-taxon IBI by sampling across a gradient of exotic cover; (2) investigate the robustness of the IBI by comparing its performance, as well as the individual metrics, with changes in sampling effort and during a drought; and (3) investigate how many levels of disturbance the IBI could distinguish. Management agencies were interested in the ability of the IBI to categorize sites into broad levels of integrity.

2. Materials and methods

2.1. Disturbance gradient

Unlike aquatic IBIs that use abiotic variables (water quality, impervious area, etc.) to estimate disturbance, most terrestrial IBIs use biological variables to estimate disturbance and carefully chosen, independent, variables to estimate biological response (Bradford et al., 1998; Brooks et al., 1998; O'Connell et al., 2000). We did the same because land use histories for study sites (e.g. grazing, fire, and agricultural) did not exist or had insufficient spatial resolution to rank sites. We used the percent cover of exotic plant species (exotic cover, EC) as a relative measure of past disturbance based on studies indicating increased exotic plants, primarily European annual grasses, following fire (Callaway and Davis, 1993; Zedler, 1995; Keeley, 2004), grazing (McBride, 1974; Minnich, 1982; Van Vuren and Coblentz, 1987), and mechanical disturbance (Zink et al., 1995; Stylinski and Allen, 1999) in CSS and related shrublands.

We focused solely on disturbance affecting vegetation for two reasons. First, the large size of many reserves may lessen the influence of edge and fragmentation effects relative to processes altering the vegetation community. Second, many managers we spoke to performed vegetation management and wanted a tool to gauge the impacts of their efforts. In addition, the types of disturbance associated with increased exotic spread (especially fire) are common in southern California shrublands.

2.2. Study areas and sampling design

We sampled Chino Hills State Park (CHSP), Rancho Jamul Ecological Reserve (RJER), and the Orange County Coastal Reserves (OCCR, Supplementary Material 1: Study sites.doc). These reserves are ~200 km apart because we wanted a broadly applicable IBI not overly influenced by local conditions.

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We initially selected 38 sites at the three locations using three criteria. First, sites were adjacent to United States Geological Survey (USGS) herpetofauna arrays to allow the use of data from the USGS monitoring program. Second, sites had to fit into a gradient of disturbance. Third, to avoid short-term fire effects (Keeley and Keeley, 1984; Malanson and Westman, 1985), we chose sites at least 9 years post-fire. We judged degraded sites as former CSS rather than other vegetation communities if we found remnant CSS shrubs, but not species indicative of riparian, chaparral, or perennial bunchgrass communities.

Sample timing and effort varied with taxa. We sampled ants, birds, and small mammals synchronously four times per year in late January–mid-February, mid-April–early May, June, and mid-September–early October in 2002 and 2003. This timing avoided hot summer months with low detection rates but still allowed replication within a year. Plants were sampled annually each spring when most annuals and perennials were at or near their phenological peak.

Fires forced us to alter sampling and statistical strategies. We stopped work at CHSP after seven of nine sites burned in 2002 (Supplementary Material 1: Study sites.doc), while nine sites at RJER burned just before the last sampling session (September 2003). After sampling vegetation in 2002, we identified a lack of sites with EC between ~60–80% (Fig. 1). In 2003, we added 10 new sites, replacing those lost to fire and adding sites with EC between 60–80% EC (Fig. 1; Supplementary Material 1: Study Sites.doc). In summary, we sampled 21 sites in both 2002 and 2003 (all eight sessions) and 26 sites for seven of eight sessions; 32 sites for all four sessions in 2002; 27 sites for all four sessions in 2003, but 36 sites for three of the four sessions in 2003. To maximize sample sizes, while assuring all sites within a dataset had identical levels of sampling, we analysed the 32-site, four-session data from 2002, the 36-site, three-session data from 2003, and the 26-site, seven-session data across both 2002 and 2003. We label these datasets "2002", "2003", and "Combined".

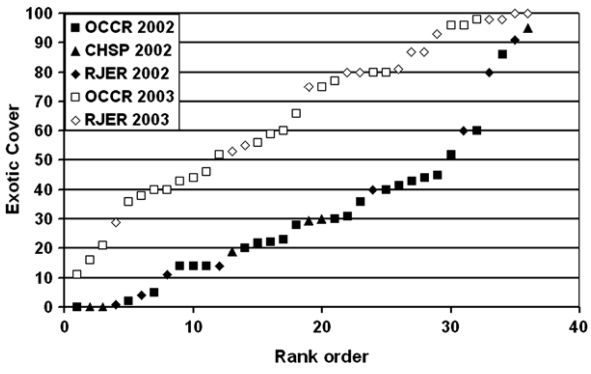

Fig. 1 – Rank order of study sites by exotic cover in 2002 and 2003. Sites are coded by site and year. OCCR = Orange County Coastal Reserves; CHSP = Chino Hills State Park; RJER = Rancho Jamul Ecological Reserve. Notice the gap between 60% and 80% absolute exotic cover in 2002. A drought in 2002 caused the low exotic cover via reduced germination and growth and highlights the dynamic nature of exotic invasion in CSS.

2.3. *Sampling techniques and spatial scale*

IBIs measure responses at defined spatial scales (Niemi et al., 2004). We chose 50 × 50 m sites (Supplementary Material 1: Study Sites.doc) because managers indicated their activities (exotic control, planting, erosion control, grazing/mowing), occurred at "hillside to hillside" spatial scales; what a work crew could achieve in a day to a week. In addition, patches of CSS intergrade with exotic-dominated habitat from 10's to 100's of square meters so our plot size allowed us to fit sites within continuous patches of a single disturbance level.

2.3.1. *Ants*

We used 6, 3-in. diameter and 2-in. deep, plastic cafeteria "Nappie" bowls buried at ground level and open during 4-day small mammal trapping sessions (Supplementary Material 1: Study Sites.doc). Ants were combined across bowls, placed on ice and stored at ~−80 °C before sorting and pinning. We counted individuals sorted to genus or species.

2.3.2. *Birds*

One of us (REC) conducted all 7-min, 100-m radius point counts from 30 min before sunrise to 10:00 a.m. Point counts began with a 2-min wait, after which any species (migrant or resident) seen or heard, and the number of individuals, were recorded. Raptors, crows, ravens, flyovers, and shore birds were not analysed.

2.3.3. *Herpetofauna*

We used herpetofauna data opportunistically. USGS sampled herpetofauna using drift fence arrays (Fisher et al., 2002) within 50 m of our sites from 1998 to 2003 while we sampled in 2002 and 2003. We sampled synchronously with USGS at OCCR for sessions 1–5. At RJER, USGS completed 1 year of sampling 3 weeks before we began. Because all sites were sampled minimally for 1 year, many for 2 years, and in most cases sampling occurred simultaneously across reserves, we felt comparisons across the gradient were reasonable.

2.3.4. *Small mammals*

We conducted 4-day trapping periods on 7 × 7 trap grids with 7 m spacing (Supplementary Material 1: Study Sites.doc) and completed all sites in ~2 weeks for each session. The trap spacing allowed us to place 49 traps within the established 50 × 50 m sites, which we felt would increase our detection rates relative to wider trap spacing. We opened, set, and baited all Sherman XLK folding traps with roasted (to prevent germination) sunflower seeds 1–3 h before dusk, closed traps after morning checks, and covered traps with wood shingles for protection from sun and rain. At each capture we recorded date, trap location, species, weight, gender, age, sexual characteristics, and a unique toe-clip (assigned on first capture).

2.3.5. *Vegetation*

All sites included 4, 50 m transects separated by 7 or 14 m. We used a point-intercept sampling method with points spaced every 2 m (Supplementary Material 1: Study Sites.doc) to measure plant cover. We estimated "absolute" percent cover by origin (native or exotic) and growth form (grasses, forbs, and woody species) as the number of points where at least one

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instance of a plant type (e.g. exotic grass) was recorded, divided by the total number of points (100). Unlike relative cover estimates, our absolute estimates of exotic and native plant cover were not inherently mathematically related. Thus, any native plant cover metrics selected would be independent from the EC gradient.

We estimated species richness for the entire site by noting species visible from the four vegetation transects and seven mammal trapping lines. In 2002, herb germination and cover were low due to drought. We sampled again in 2003, a year approaching mean rainfall, and used these data in our analyses, except four sites sampled in 2002 and then burned. Given the annual sampling strategy for plants, 46 sites were sampled for plants despite fires.

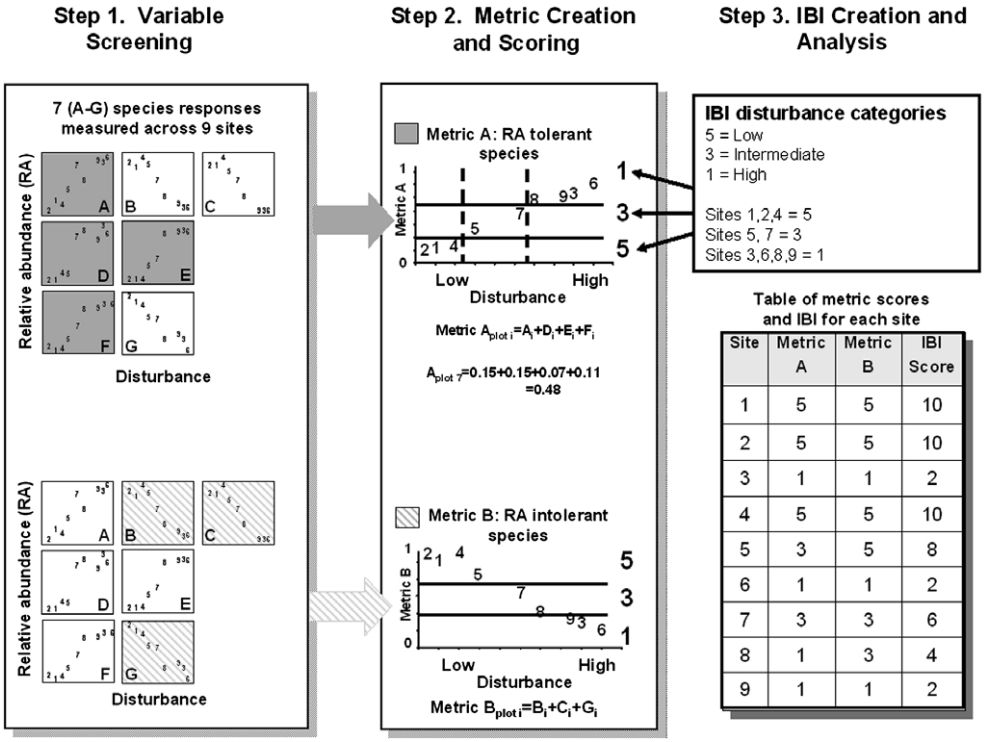
2.4. *Data analysis and IBI development*

2.4.1. *Step 1. Variable screening*

For IBI development, we followed methods described in Karr and Chu (1999), which fell into three general steps (Fig. 2). First, as strongly suggested by Karr and Chu (1999), we identified metrics by visually inspecting scatterplots of variables (e.g. richness, relative abundance, etc.) across the EC gradient (Fig. 2). We attempted to base IBI metrics on species-level data but combined data within a genus (or plant type) if species level trends were not apparent. We looked for obvious thresholds in presence and absence across the gradient or large changes in the proportion of sites occupied (e.g. 8 of 10 occurrences from 0% to 20% EC vs. 2 of 10 from 70% to 100% EC). When we observed an obvious response, we checked for similar responses across datasets and reserves and only used variables consistent across both. Given space constraints, we give an example of this procedure using ants (Supplementary Material 2: Metric screening for Ants.doc), but report only the IBI metrics created from the process.

2.4.2. *Step 2. IBI metric creation and scoring*

We investigated species and genus richness as potential metrics and vegetation variables related to cover and structure. In addition, we attempted to create four types of metrics for each taxon. The proportion of tolerant species and the proportion of intolerant species (or genera) were the number of species at a site with positive (tolerant) or negative (intolerant) responses in presence–absence across the EC gradient



Site	Metric A	Metric B	IBI Score
1	5	5	10
2	5	5	10
3	1	1	2
4	5	5	10
5	3	5	8
6	1	1	2
7	3	3	6
8	1	3	4
9	1	1	2

Fig. 2 – Three general steps in IBI creation. In step 1 a hypothetical taxon with 7 species is screened to make to two IBI metrics. Each scatterplot represents the relative abundance (RA) of a species (A–G) vs. disturbance at 9 study sites (1–9). For Metric A, species A, D, E, and F are selected and show increases in RA with increased disturbance. For Metric B, species B, C, and G are selected and show declines. In step 2, RA values are summed across the selected species to create site-specific metric scores. These site specific metric scores are then plotted against the original disturbance gradient (shown for A and B with sites labeled uniquely). The metric is then categorized using the 1,3,5 scoring system recommended in Karr and Chu (1999). In metric A, a line separates sites 1,2, and 4 as low disturbance sites. These sites are given a score of 5 to represent low disturbance or high integrity. Another threshold separates sites 3, 6, 8 and 9 as low integrity sites, with a score of 1. Sites 5 and 7 have intermediate scores for Metric A and are given a score of 3. In this example, the thresholds on the y-axis resulted in no overlap of points along the x-axis (see the dashed vertical lines). In Step 3, the IBI is created by summing the individual metric scores for each site.

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divided by the total number of species detected at a site. For example, if 10 species occurred at a site and five were intolerant (showed declines with increasing EC), the proportion intolerant would equal 0.5. We also calculated the "relative abundance of tolerant species" and the "relative abundance of intolerant species" by summing the relative abundances of those species with positive or negative responses to increasing EC. Relative abundance was the total number of individuals detected of a species divided by the total number of individuals detected across all species within a taxon. In summary, the proportion tolerant or intolerant species metrics used species presence–not-detected data, while the relative abundance metrics used counts of individuals across species.

We also investigated absolute cover of native vegetation, woody vegetation (live, dead, and total), and the average maximum height and richness of native shrubs as potential IBI metrics. Our exploratory data analysis resulted in a total of 31 potential metrics (ants, birds, herpetofauna, small mammals, and vegetation $n = 5$ taxa $\times 4$ tolerant/intolerant metrics + 6 richness metrics + 5 summary plant metrics, Table 1).

We graphically explored potential metrics across increasing levels of EC. When metrics showed a response across the gradient, we broke the metric into three categories and scored sites using the 1, 3, 5 system suggested by Karr and Chu (1999) where 1 denoted highly disturbed sites, 3 moderately disturbed, and 5 undisturbed (Fig. 2). The placement of category boundaries (i.e. metric thresholds) is arbitrary (Karr and Chu, 1999) but should create a functional and repeatable IBI. Once in place, these boundaries are used by future implementations of the IBI to assure consistency. We created metric thresholds so that sites never overlapped between low and high disturbance categories on the disturbance gradient, though some overlap occurred between low and intermediate, and intermediate and high categories (Fig. 2). For example, a categorization could have resulted in sites within the high disturbance category (score = 1) having EC values ranging from 0.7 to 1.00 and sites with intermediate disturbance (scores = 3) having EC values from 0.4 to 0.8. In this case, a few sites with a disturbance score of 1 actually had lower EC values than sites in with a score of 3. Our categorization never let this occur between low and high disturbance sites. The final IBI was simply the sum of the individual metric scores for each site.

2.4.3. *Step 3. Testing IBI performance*

All analyses were performed in Systat v10.0 or SPSS v14. We used estimates of relative abundance or presence–not-detected unadjusted for differences in detection probabilities, as have all other IBIs we know of (Karr and Chu, 1999; Glennon and Porter, 2005), and assumed biases caused by detection differences were relatively small and had little impact on IBI performance. However, we checked the adequacy of our sampling effort with curves of metric performance. These were analogous to species accumulation curves, but were created for each metric except those from plants (only sampled twice). For each site, we calculated the metric at varying levels of cumulative sampling effort then plotted this value against the number of sampling sessions. We expected the curves for each site to asymptote within increasing sampling effort.

We performed a series of analyses to examine IBI performance and stability. First, we confirmed the relationship of the IBI to the disturbance gradient by regression of the IBI against EC. Second, we examined IBI stability using paired *t*-tests to check for statistically significant (Bonferroni corrected) changes in site-specific IBI scores across years with (2002) and without drought (2003), or with 1 vs. 2 years of sampling (2002 or 2003 vs. combined). Finally, for comparison with the IBI, we correlated patterns in species richness, a metric used in prior work related to CSS monitoring (Chase et al., 2000) with EC for each taxon.

We used cluster analysis and follow-up ANOVAs to determine how many levels, or categories, of disturbance the IBI could distinguish. Cluster analyses utilized squared Euclidean distance and Ward linkage agglomeration on the 15 IBI metric scores to define clusters of sites having similar patterns of individual metrics. We found no multivariate outliers and low correlations among all but three variables so we retained all metrics. Follow-up one-way ANOVAs compared mean IBI scores among the resultant clusters.

The clustering followed by ANOVA approach was employed because we were concerned sites could have identical overall IBI scores, yet different patterns of scores across metrics. For example, in a five metric IBI, a site could have scores of (1, 1, 1, 5, 5), (5, 5, 1, 1, 1), or (3, 3, 3, 3, 1) yet have the same IBI score (13). A non-significant ANOVA would indicate the cluster algorithm placed sites in different categories based on patterns of individual metric scores, despite similar IBI scores, complicating interpretation of disturbance categories.

Table 1 – Potential and used metrics

Taxon	Metric type					
	Proportion intolerant	Proportion tolerant	Rel. abund intolerant	Rel. abund. tolerant	Richness	Other
Ants	√	√				
Birds	√	√	√	√		
Herpetofauna	√	√	√			
Mammals	√		√		√	
Vegetation		√			√	Absolute woody cover

The 15 metrics included in the CSS-IBI by taxon and metric type. All metrics were created using species-level data except for ants (Genera). Five summary plant metrics investigated as potential metrics were: absolute cover of woody (included as a metric), all natives, live woody, and dead woody vegetation, and the average maximum height of native shrubs.

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Alternatively, significant differences among clusters in their mean IBI would indicate the clusters differ in both their pattern of metric scores and their overall IBI. Thus, the combined analyses helped determine how many categories of disturbance the IBI could distinguish (O'Connell et al., 2000).

Finally, to better understand the biological response to the disturbance gradient, we used ANOVA to examine differences across the cluster categories for each of the 15 IBI metrics. In all ANOVAs, individual sites were the unit of replication.

3. Results

3.1. Metric screening, selection, and scoring

We observed numerous responses to the EC gradient but do not report all scatterplots (>2100). Ants serve to illustrate the metric creation process (Supplementary Material 2: Metric screening for Ants.doc). The remaining IBI metrics are reported in Supplementary Material 3: 15 IBI metric summary and scoring.doc.

3.1.1. Ants

We captured 5154 individuals, identified 18 genera, 16 species, and created two metrics. Few species responded to the EC gradient so we created no metrics from species-level data. The genera-level data generated the proportion of tolerant and intolerant genera (Fig. 3). *Dorymyrmex*, *Formica*, *Linepithema*, and *Myrmecocystus* were not found on sites with EC greater than approximately 65, 80, 60, and 65, respectively (Supplementary Material 2: Metric screening for Ants.doc). *Messor*, *Pogonomyrmex*, and *Tetramorium* genera only occurred on sites with EC levels greater than approximately 40, 40, and 35, respectively. *Pheidole* occurred at higher proportions on sites with more than 60 EC.

3.1.2. Birds

We detected 2472 individuals of 33 species and created four metrics. Seven species showed negative (intolerant) and seven showed positive (tolerant) responses in presence/absence, resulting in two metrics: the proportion of intolerant and tolerant species. These metrics separated high EC sites from other sites. In addition, we used five and eight species for intolerant and tolerant metrics based on relative abundance. The relative abundance of intolerant species separated all disturbance categories. The relative abundance of tolerant species was low (0–0.4), but distinguished low from high EC sites.

3.1.3. Herpetofauna

USGS personnel detected 1183 individuals of 27 species and we created three metrics. The proportion of six intolerant species declined linearly with higher EC and separated low and high EC sites. The proportion of five tolerant species weakly discriminated low from high levels of disturbance. Finally, the relative abundance of intolerant species included four species and separated intact (low EC) sites from all others.

3.1.4. Mammals

We captured 3778 individuals across 14 species and created three metrics. The overall richness of eight common native species declined with increasing EC and separated highly disturbed sites from others. The proportion of four tolerant species separated all EC categories and the relative abundance of three intolerant species separated low and high levels of disturbance.

3.1.5. Vegetation

We developed three IBI metrics after screening 214 species for trends in presence–absence. First, absolute woody cover declined sharply across the gradient and separated all levels of EC. Second, native woody species richness separated high from low EC sites. Third, we included 28 species in a proportion tolerant species metric, which weakly separated high and low EC sites.

3.2. Metric performance and sampling effort

We evaluated the performance of the 12 animal metrics by creating site-specific curves of the metric value with increasing levels of sampling effort, then plotting all sites on the same graph. We expected the metric value at any given site to reach an asymptote as sampling effort increased and sample sizes became larger, while the range of asymptotic values across sites would reflect the change in the metric across the sampled disturbance gradient. Metric values for a site generally

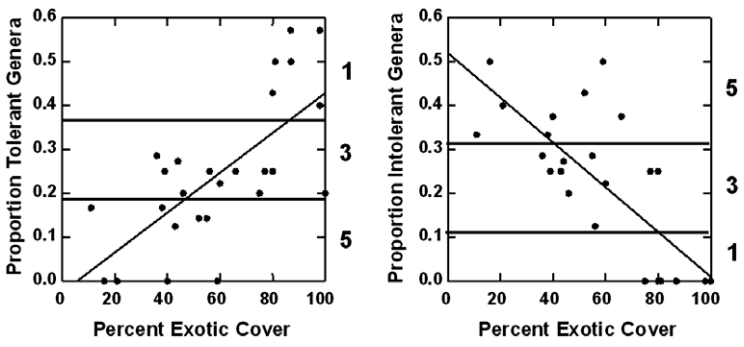

Fig. 3 – Two of 15 IBI metrics used in the IBI. Proportion tolerant and intolerant ant genera versus percent exotic cover. Horizontal lines demarcate 1, 3, 5 are scoring categories for each metric, while the diagonal lines from least-squares regression. Individual genera scatterplots are in Supplementary Material 2: Metric screening for Ants.doc.

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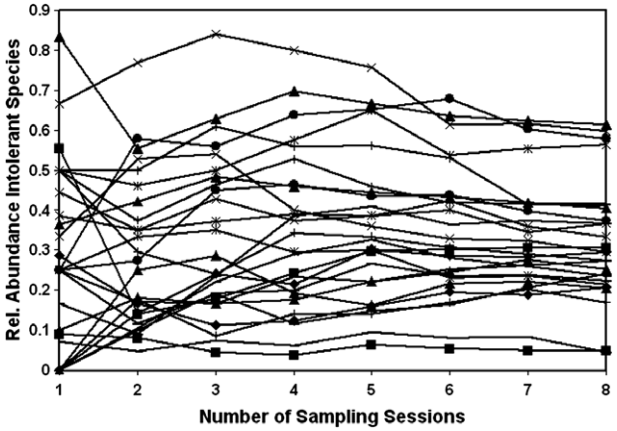

Fig. 4 – Performance curves for the relative abundance of intolerant bird species. Each line represents a unique site (thus no legend) and we only plot those sites with eight sampling sessions. Two patterns emerge. First, metric values for individual sites reach asymptotic values with low amounts of variation within ~4 sampling sessions. Second, the range of values in relative abundance across sites (i.e. the vertical spread of the site-specific values) is much larger than the variability present at any given site after four sampling sessions.

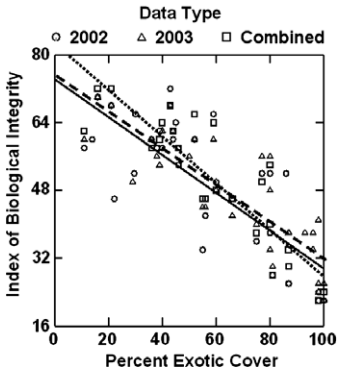

Fig. 5 – The 15 metric IBI vs. Percent Exotic Cover. Lines represent the least-squares regression for 2002 (solid), 2003 (dashed), and combined (dotted) data. The IBI is limited in range from 15 to 75.

changed as sampling effort increased from 1 to 3 sessions (Fig. 4, Supplementary Material 4: IBI metric performance curves). However, for nearly all sites and all metrics, values reached asymptotes after four or five sampling sessions. In the case of intolerant bird relative abundance (Fig. 4), variation in both the numerator (total # of individuals of intolerant bird species) and denominator (total # of all individuals) occurred with minimal sampling effort, and is observed in the large changes within a site during the first 1–4 sessions. However, after four sessions, sample sizes became larger for both numerator and denominator so this ratio varied less.

Critical to IBI performance, the range of asymptotic metric values across the sites was far greater than variation within any given site. This indicated the observed variation in the metric across the gradient (i.e. the vertical range of metric values shown in the graphs) was much greater than variation caused by sampling error. Since metrics were binned into three broad categories for the IBI, only a very small proportion of sites would change their 1, 3, 5 categorization after four sampling sessions. These analyses indicated 1 year (four sessions), and particularly 2 years, of sampling resulted in stable metrics.

3.3. *IBI performance and stability*

3.3.1. *IBI performance*

We created an IBI by summing the 15 metric scores (1, 3, or 5) for each site (Supplementary Material 5: Site specific IBI scores.doc). The IBI ranged from 21 to 67 (possible range 15–75) and showed a strong relationship with the disturbance gradient (Fig. 5). Data combined across years, despite a smaller sample size, showed a slightly better fit than either 2002 or 2003 data though slopes and intercepts were similar (Combined: IBI = −0.51EC + 76.96, R^2 adj = 0.753, $n = 26$, $p < 0.001$; 2002: IBI = −0.42EC + 70.61, R^2 adj = 0.588, $n = 32$, $p < 0.001$; 2003: IBI = −0.41EC + 70.00, R^2 adj = 0.714, $n = 36$, $p < 0.001$, Fig. 5). The IBI was stable over climatic variation and with differing levels of sampling as paired *t*-tests found no differences in IBI scores across the three datasets. This finding was also consistent with the general stability of individual metrics after just four sampling sessions.

3.4. *Taxon responses and richness patterns*

We observed variation in patterns of within-taxa richness across the EC gradient. Animal taxa showed no statistically significant correlations in observed richness across sites in any dataset. Small mammal and native woody richness were positively correlated in 2002 ($r = 0.542$, $n = 32$, $p = 0.001$) and 2003 only ($r = 0.510$, $n = 36$, $p = 0.002$) (Supplementary Material 6: Taxon correlations.doc). Bird and native woody richness were positively correlated in 2002 only ($r = 0.355$, $n = 32$, $p = 0.047$). Finally, native plant richness and native woody richness were positively correlated in all datasets (2002: $r = 0.915$, $n = 32$, $p < 0.001$; 2003: $r = 0.631$, $n = 36$, $p < 0.001$; Combined: $r = 0.648$, $n = 26$, $p < 0.001$).

Reflecting the lack of correlations in richness between animal taxa, we observed variation in patterns of richness across the EC gradient (Supplementary Material 6: Taxon correlations.doc). Bird and herpetofauna richness did not change across the EC gradient, while ant richness increased with increasing EC in 2003 only ($r = 0.394$, $n = 36$, $p = 0.017$). Small mammal richness declined with increasing EC (2002: $r = -0.393$, $n = 32$, $p = 0.026$; 2003: $r = -0.582$, $n = 36$, $p < 0.001$; Combined: $r = -0.422$, $n = 26$, $p = 0.032$). We found a strong negative relationship between percent exotic cover (EC) and both native cover (NC) and woody cover (WC) (NC = −0.578 (EC) + 104.7, $n = 46$, $p < 0.001$, $R^2 = 0.416$. WC = −0.778(EC) + 104.0, $n = 46$, $p < 0.001$, $R^2 = 0.647$).

3.4.1. *Cluster analysis*

Clustering algorithms produced well-supported four-cluster solutions (Fig. 6) and mean IBI scores differed across all four

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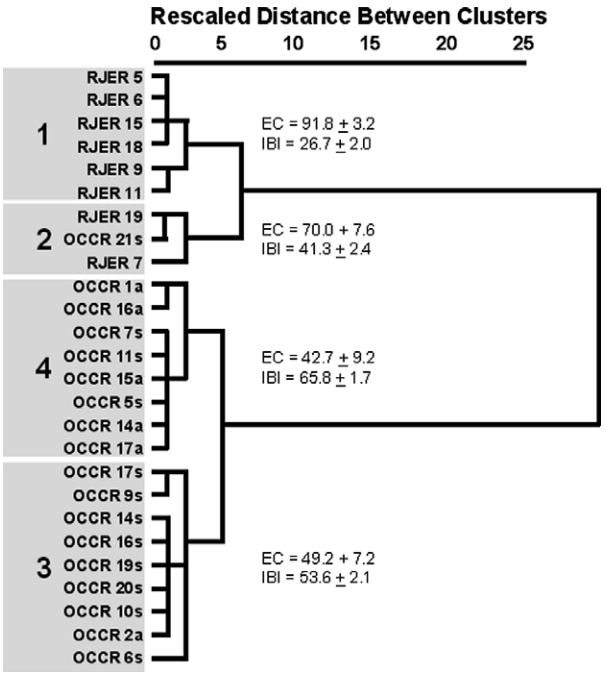

Fig. 6 – Dendrogram from cluster analysis for the combined dataset. The four grayed clusters were used as categories in the ANOVAs testing for differences in the individual IBI metrics. The numeric label for each cluster relates to the four integrity categories as follows: 4 = highest; 3 = high; 2 = medium; 1 = low.

clusters in 2002 ($F_{3,28} = 69.181$, $p < 0.001$), 2003 ($F_{3,32} = 52.432$, $p < 0.001$), and with the combined data ($F_{3,22} = 65.488$, $p < 0.001$, Supplementary Material 7: Cluster analysis results.doc). The four clusters represented groups of sites with similar patterns of individual metric scores and similar IBIs and, thus, relatively distinct disturbance categories. We labeled the four categories as "highest", "high", "medium" and "low" integrity based on their mean IBI score.

3.5. *Biological responses across the EC gradient*

Means of individual metrics typically varied across two or three, but never all four cluster categories, indicating the ability of the IBI to discriminate among four levels of disturbance relied on the additive effects of the 15 metrics (see table, Supplementary Material 7: Cluster analysis results.doc). Interestingly, EC did not vary across all clusters. In 2002, mean EC of low integrity sites differed from highest and high, but not medium integrity sites ($F_{3,28} = 7.327$, $p = 0.001$). In 2003, highest and high integrity sites had similar mean EC, as did medium and low sites ($F_{3,32} = 13.75$, $p < 0.001$). With the combined data, highest and high sites had similar mean EC, while medium integrity sites did not differ from other sites ($F_{3,22} = 7.881$, $p = 0.001$). This indicates that IBI may be a more sensitive measure of disturbance than EC or any subset of metrics alone.

Summarizing across datasets, low integrity sites showed the greatest differences from the other three categories (Supplementary Material 7: Cluster analysis results.doc). On average, they supported lower woody cover and more tolerant species though they supported the same low level of native woody richness as medium integrity sites. Low integrity sites differed from highest and high integrity sites in 9 of 12 animal-based metrics, had no tolerant ant genera and extremely low relative abundances of intolerant mammals. Low integrity sites had greater proportions of grassland birds, tolerant herpetofauna, and tolerant small mammals than medium integrity sites.

Medium integrity sites had less shrub cover and native woody richness than high and highest integrity sites but had similar levels of tolerant plant species. These sites were exotic grasslands with sparse shrubs and had more woody cover than low integrity sites. Medium integrity sites differed from highest integrity sites in 8 of 12 animal-based metrics. Compared to high integrity sites, medium sites had lower relative abundances of intolerant small mammals and woody birds, lower proportions of woody bird species and intolerant ant genera and higher proportions of tolerant herpetofauna species.

Highest and high integrity sites showed the fewest differences across individual metrics despite differences in mean IBI scores. Across all datasets, highest integrity sites had a greater proportion of intolerant ant genera and a lower proportion of tolerant ant genera than high integrity sites, but all other metrics were not statistically distinguishable. Despite the lack of statistically significant differences for 13 of 15 metrics, highest integrity sites nearly always had higher mean values for metrics based on intolerant species, woody cover and native woody richness, and lower mean values for metrics based on tolerant species. When converted into the 1, 3, 5 scoring system, more highest integrity sites were given 5's than high integrity sites across metrics, which resulted in statistically significant differences in the mean IBI across clusters. Interestingly exotic species were often present at these sites at levels higher than we expected (EC values ~35–45%). This indicates that many CSS specialists are tolerant to exotic grass invasion if shrub structure remains intact.

4. Discussion

4.1. *Community level indices vs. IBIs*

Using common community metrics, we found a variety of responses across the disturbance gradient. Species richness of mammals and woody plants declined across the gradient while birds, ants, and herpetofauna showed no changes. In addition, individual species increased, decreased, or showed little change across the gradient. When combined with previous work on single species indicators in CSS (Chase et al., 1998; Chase et al., 2000; Case and Fisher, 2001; Rubinoff, 2001) these inconsistent responses strongly argue: (1) general metrics of community structure (e.g. richness) are poor indicators of condition in CSS; (2) no taxa will serve as an indicator for the others; and (3) finding a successful indicator or umbrella species is highly unlikely.

Our IBI, as well as the Bird Community Index (Brooks et al., 1998; O'Connell et al., 2000; Glennon and Porter, 2005), indicate terrestrial, index-based methods of assessment are

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viable methods in monitoring programs. In CSS, the index-based approach is an improvement over single-species or indicator-based approaches for two reasons. First, responses to disturbance are complex and not correlated across taxa so the response of any single species (or even single taxon) captures little information regarding the total system response. Second, the biotic and abiotic conditions within CSS vary at multiple spatial scales. CSS has both large scale variation caused by moisture and rainfall gradients (Westman, 1981; DeSimone and Burk, 1992; Chase et al., 2000) and mosaics of shrub associations and patches of exotic grasses at scales of 10–100 m^2 (DeSimone and Burk, 1992). Furthermore, we observed dynamic levels of exotic invasion driven by annual rainfall (Fig. 1). These patterns of variability decrease the likelihood a single species will correlate with general patterns of diversity as different species utilize habitat and landscapes at different spatial scales (Kareiva, 1990; Ims, 1995; Diffendorfer et al., 1999).

We suspect these two conditions, variable responses of species to anthropogenic disturbance and variation across multiple spatial scales, are common across many terrestrial ecosystems and habitats. If so, IBI-based approaches should be effective in a broad array of terrestrial systems because their development requires measuring system-specific 'ecological dose response curves' (Karr and Chu, 1999) during metric development. This process effectively tailors metric selection and measured responses to the system of interest. Furthermore, our data suggests that by combining information across a large number of species the technique detects signals in system response not identified by more general or traditional, community variables. This allows a more comprehensive measure of an intact community.

4.2. *Biological changes across the gradient*

Karr and Chu (1999) indicate one 'myth' of IBIs is that they combine and thus lose information. However, IBIs can be decomposed into their individual metrics to understand biological responses across the gradient in detail. Cluster analyses indicated four integrity categories could be extracted from the individual metric scores. Comparing the individual metrics across these categories and the species or genera making up each metric helped us understand how the system responded to disturbance.

Two aspects of our analyses suggest the IBI was sensitive to disturbance beyond just increases in exotic grass invasion. First, mean values of EC did not vary across all four of the integrity categories created by the cluster analysis, though the IBI did. This indicates the multivariate clustering of sites was not fully driven by changes in EC. Second, though our intolerant metrics were composed of species known to occur primarily in CSS, our tolerant metrics included grassland specialists, species that occur in open or disturbed CSS, habitat generalists, and species that are relatively unaffected by anthropogenic influences. For example, of the 28 tolerant plant species 25% were legumes, a plant group including well-known colonizers of disturbed sites (O'Leary, 1982) while other tolerant plants species occur in CSS, grasslands, oak woodlands and a variety of disturbed habitats.

Thus, the IBI measured two general responses across the gradient, the loss of species dependent on CSS and the addition of species associated with disturbed CSS or grassland specialists. Low integrity sites were highly disturbed, contained almost no shrub cover and were dominated by disturbance prone and grass favoring species. CSS specialists were rarely detected on these sites. Medium integrity sites were dominated by exotic grasses but had sparse shrubs. This low shrub cover resulted in infrequent use by CSS species, such as small mammals. Simultaneously, these sites still supported the vast majority of grassland specialists and disturbance prone species. High and highest integrity sites were dominated by CSS specialists and had low relative abundances and few occurrences of grassland or disturbance prone species.

4.3. *IBI implementation*

The relatively small spatial scale (~2500 m^2 area) of the CSS-IBI impacts its use in management. This scale was based on discussions with managers regarding the size of areas affected by management programs and the scales of variation in disturbance-facilitated grass invasion. We see three possible applications of terrestrial IBIs. First, monitoring or understanding the impacts of various management and restoration actions can be achieved using before/after or treatment/control designs. Second, IBIs can be used to monitor the impacts of, and recovery from, fire or other forms of disturbance. Third, when arrayed across single or multiple reserves and sampled through time, an IBI can measure both spatial and temporal variability in overall integrity.

Reserve-wide applications of IBIs measured on smaller study sites will yield information on spatial and temporal variation in integrity and provide valuable information towards large-scale conservation and management. Given the rate of change in species composition, structure, and function of terrestrial systems, temporal sampling in large-scale monitoring may only be necessary at intervals ranging from 3 to 10 years depending on the system. However, IBIs are tailored to specific habitat types, and a given spatial scale, while a reserve may contain many habitat types. The IBI we developed is specific to CSS and the suite of species sampled. It likely does not measure processes occurring at larger spatial scales, such as isolation impacts on large carnivores (Crooks, 2002) or the role of riparian corridors for breeding birds. Thus, if managers are interested in monitoring species whose life-cycles integrate multiple habitat types, the IBI framework is general enough to allow scale-appropriate IBI development specific to a management need.

Our use of multiple taxa is different from most IBIs, which typically use data from one taxon. Niemi et al. (2004) clearly articulate how multiple stressors impact systems and how indicators must clearly link system response to such stressors. They argue the use of multiple taxa increases the scope and sensitivity of biological indicators. However, despite calls for the use of additional taxa in IBIs (Karr, 1993) few have done so.

The ecological context and use of an IBI should dictate the types and number of taxa utilized. We feel the decision to use multiple taxa should depend on how well the response to disturbance is understood and IBI performance issues related to sampling. The strength of IBIs is their ability to incorporate

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many attributes of the biological community into a repeatable measure (Karr et al., 1986; Kerans and Karr, 1994; Fore et al., 1996; Brooks et al., 1998; O'Connell et al., 2000). Thus, in systems where response to disturbance is well understood, a single-taxon IBI is a cost-effective method for monitoring. On the other hand, in systems where response to disturbance is poorly understood, or varies greatly across taxa, incorporating multiple taxa should increase the ability of the IBI to measure degradation and instills confidence the IBI truly measures overall system response.

Sampling issues may also advocate multi-taxon approaches in terrestrial systems. Unlike aquatic IBIs where a few siene hauls or D-net samples can capture 100's of individuals of many species, our sampling effort did not yield abundant and species-rich samples. For example, regularly trapped small mammals consisted of only eight species, not enough to develop an IBI. Even birds, diverse and easily sampled, produced sparse data. Thus, we had to utilize data from many taxa to develop the IBI. We anticipate similar situations will occur in other terrestrial systems, particularly where taxonomic expertise for arthropods, typically the most diverse taxon, is lacking.

One potential drawback to a multi-taxon IBI is cost. Clearly sampling a wide array of taxa may be prohibitively expensive for some entities. In our work, the main cost involved supporting a team of biologists with a wide variety of taxonomic expertise. Our experiences with agencies in southern California indicate most typically fund taxon-specific monitoring, sometimes with taxon-specific management goals in mind, but also as general assessments. Thus, the same agency, or suites of agencies may support bird surveys at some reserves, plant monitoring at others, while also sampling herpetofauna and small mammals. At an agency level or across a reserve system, a comprehensive monitoring plan that samples multiple taxa at the same locations may actually cost the same (or less) than the sum of disparate, individual monitoring efforts. Furthermore, a comprehensive monitoring approach creates the opportunity for centralized data management and the synthetic development of an IBI.

4.4. *Broader implications*

Our work indicates a broad array of species rely on CSS vegetation and reinforces its role in maintaining diversity in southern California. The results convincingly show a unique suite of CSS-oriented species drop out of sites as levels of exotic cover increase and shrub cover declines. They also indicate that traditional metrics of community structure do not describe these changes well and should not be used in monitoring efforts. Given the myriad of studies linking disturbance to vegetation change in CSS (Minnich, 1982; Zedler, 1995; Zink et al., 1995; Stylinski and Allen, 1999), our results show a strong empirical link between disturbance and the taxonomic composition of CSS.

In particular, frequent fires (1–3 year return intervals) can reduce shrub cover and increase non-native plants (Zedler and Scheid, 1988; Haidinger and Keeley, 1993; Zedler, 1995) and have been associated with the conversion of CSS to grassland (Keeley, 1990; Callaway and Davis, 1993). During our 2-year study, 12 of our original 38 study sites (31%) burned. Furthermore, catastrophic fires in 2003 burned over 46,000 hectares of CSS, ranging from 6% to 89% of the CSS in various reserves. The gradient we sampled mimicked the vegetation changes associated with CSS conversion to exotic grasslands by frequent fires. As such, the large declines in shrub related species we observed across the gradient can likely be generalized to fire-induced changes in CSS.

Our results suggest maintaining CSS despite increasing ignitions (Keeley and Fotheringham, 2001) is critical to maintaining diverse communities of CSS favoring species. Managers must develop strategies that reduce burn frequencies within reserves, reduce the spread of fires into reserves, and increase the speed of controlling fires in reserves, as detailed in previous publications (Keeley, 2002). Prescribed burns need careful consideration regarding how they increase long-term fire return intervals. Furthermore, minimizing activities that can either reduce shrub cover or increase exotic spread (i.e. edge effects, illegal off-road vehicles, and unauthorized trail creation) is warranted. Finally, largely unstudied strategies for facilitating CSS recovery after disturbance (such as reseeding) may be as important as controlling exotic grasses since shrub specialists responded strongly to losses in shrub cover and even our highest integrity sites contained exotic species.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.biocon.2007.08.005.

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