Coastal Sage Scrub response to disturbance. A literature review and annotated bibliography

Prepared for:
California Department of Fish and Game

James E. Diffendorfer, Robert E. Chapman, Jennifer M. Duggan, Genie M. Fleming, Milan Mitrovitch, Matthew E. Rahn, and Rosalie del Rosario

Department of Biology
San Diego State University
5500 Campanile Drive
San Diego, CA 92182

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Executive Summary

We reviewed literature pertaining to how the vegetation, mammals, birds, arthropods, and herpetofauna of Coastal Sage Scrub (CSS) respond to disturbance. During the review process, we looked for evidence indicating these taxa, or members of the taxa, would show responses to disturbance and therefore contribute useful metrics to an Index of Biological Integrity (IBI) for CSS. As expected, the level of research, and hence the current state of knowledge regarding the natural history, ecology, and response to disturbance is highly variable across the taxa. For all taxa, a long-history (10-20 years) of well-designed research on responses to disturbance simply does not exist (if it did, this project would likely not be needed). This variation in past research and state of knowledge caused our taxa reviews to vary in structure and content.

Despite the poor state of knowledge in some cases, the review indicates responses to disturbance are measurable, obvious and quantifiable with standard field protocols for all the

taxa. As such, we are encouraged about deriving a multi-taxa IBI in the next two years as our field studies produce new data.

Of all taxa, vegetation is best studied, with a large and varied literature. Responses to fire have been well documented. Unfortunately, vegetation response to other forms of disturbance is less studied. Our review indicates invasion of CSS by nonnative grasses and forbs is highly correlated with disturbance. Furthermore, it is likely these nonnative species persist in CSS stands even after the shrub component has recovered. The response of the native, herbaceous understory to invasion is basically unknown. However, it seems likely a stand of CSS could appear intact from a distance, yet have a reduced herbaceous component replaced by nonnative grasses.

Unlike the other taxa, a number of researchers have successfully created IBI's from bird survey data. These studies, when combined with studies of CSS bird community response to habitat fragmentation and urbanization, suggest the development of an IBI for birds will be straightforward. Since birds are easily observed and much is known about habitat preferences, migration, diet, and breeding times, we include a preliminary conceptualization of a guild structure we might use when implementing a bird IBI.

Information on mammals and arthropods is somewhat limited. In the case of small mammals, a handful of studies suggest the processes structuring small mammal communities in CSS are similar to those in well-studied systems such as the desert Southwest and Australian heathlands. These studies, in concert with a few directed studies of small mammals in CSS, strongly suggest CSS mammals will show direct and rapid responses to disturbances, particularly those altering vegetation composition or structure.

Arthropods, given their massive levels of diversity, are poorly studied, yet our review found evidence suggesting Arthropod diversity and composition would change as CSS is disturbed. Methodological challenges associated with identifying species must be overcome to use Arthropods in monitoring programs. The use of morphospecies may solve this problem. If so, the large diversity of species (or morphospecies), the relative ease sampling, and the highly specified life histories of many arthropods may make it possible to discriminate between more levels of biological integrity in CSS than with the other taxa.

Our review resulted in three general recommendations. First, we need more studies elucidating responses of taxa to the most threatening forms of disturbance in reserves. In general, we do not understand how specific forms of disturbance impact CSS species. Thus, we strongly recommend directed studies on how target species, specific taxa, and food webs in CSS respond to both disturbances and possible management practices. These studies can be implemented by setting up monitoring locations across gradients in the level of disturbance (e.g. distances from edges, time since fire, level of restoration, amount of invasion, etc), or by designing experimental manipulations in particular reserves designed to answer specific questions or test hypotheses. Second, we found little support for the use of indicator species as a method for understanding or predicting community-level patterns in CSS. Indicator species may be useful in particular situations (such as a host plant for a particular species), but they rarely show a strong correlation with the rest of the community. As such they have little value in helping understand responses to disturbance or guiding management. Third, given the unique nature of CSS and the realities of reserves in an urban landscape, there are a limited number of management actions available to reserve managers. These should be prioritized and studied for their utility and cost-effectiveness.

Introduction

Rapid and sustained human population increases during the last century have increased displacement and fragmentation of southern California's (S.CA) native systems. Coastal sage scrub's (CSS) tendency to occur on relatively fertile coastal lowlands has made it particularly vulnerable to both agricultural and urban displacement. Estimates of the extent of coastal sage scrub loss range from 36% to 85% (O'Leary 1990a, 1995), with most experts agreeing with higher levels of destruction. Efforts to conserve remaining CSS have resulted in complex, large-scale efforts at reserve design and management. These efforts, driven almost exclusively by the Natural Communities Conservation Plan, are precedent setting and have received recognition at the highest levels of government.

Given: 1) the heterogeneous mix of land use patterns surrounding most of the NCCP reserves, 2) the extent to which many existing reserve lands were historically disturbed by grazing, altered fire regimes, agriculture and invasive species, and 3) strong public pressure to use these lands as parks instead of reserves for endangered and threatened species, the success of the NCCP program will rest almost solely on the ability of local reserve managers to maintain the *in-situ* biological integrity of each reserve in face of worsening external pressures. This task, though difficult, is not insurmountable if managers are given the correct tools, have high quality data to make science-based decisions, and if we understand the response of CSS food webs to both disturbance and the limited number of possible management actions feasible.

The overarching goal of the "IBI project" (i.e. the CDF&G grant to Dr. Diffendorfer "Creating and Index of Biological Integrity for Coastal Sage Scrub: A tool for habitat quality assessment and monitoring") is to develop a conceptual framework for analyzing multi-taxa monitoring data in CSS habitats. The approach, if successful, will create a method for comparing the biological integrity of different CSS sites or the same site before and after management actions. Developing a successful IBI will also help direct efforts to create and implement comprehensive, economical, and biological relevant monitoring programs in CSS throughout the NCCP reserve system.

Background: Developing Indices of Biological Integrity.

In this section, we familiarize the reader with the Index of Biological Integrity (IBI), the function it plays, and how it is developed. This general background is necessary to fully understand the information we attempted to gather during our literature review. Our other report to CDF&G (Diffendorfer et al. 2002) describes the development of IBI's and the measurement of disturbance in more detail. Readers wanting additional information on IBI's should look there.

What is biological integrity? A concept frequently mentioned in this report and in large-scale, ecosystem management (as is occurring in the NCCP) is ecological (Norton 1992), or biological integrity (Frey 1975, Woodley et al. 1993, Angermeier and Karr 1994). Biological integrity, as defined by Frey (1975), is "*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*." Biological integrity is a multifaceted concept incorporating not only components of systems (i.e. species) but also system processes (i.e. predator-prey dynamics, succession, population regulation, etc). In addition, biological integrity is a relativistic measure. A site's quality is based on how far away it is from a typical, intact system.

How is biological integrity measured? Indexes of biological integrity are used to measure biological integrity. IBI's for different systems often vary in details, such as the taxa used, or the metrics included, but the general approach used and the overall goal is similar. IBI's are developed using 4 main steps.

Step 1) Empirical studies develop species or guild response curves by sampling across gradients of disturbance. These empirical relationships are similar to dose-response curves used in toxicological studies and show how specific metrics respond to disturbance.

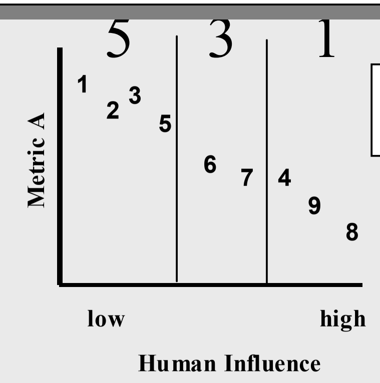
Step 2) A scoring system is developed for combining the various response curves into an easily understandable methodology. A standard approach used in most IBI's is to categorize each response curve into 3 sections, giving them a score of 1, 3 and 5, where a 1 indicates high levels of disturbance.

Step 3) A subset of metrics is chosen for the final IBI. In this step, metrics are screened to avoid including repetitive metrics measuring similar responses to disturbance. In addition, statistical analyses are performed to determine the best set of metrics to include in the IBI and the number of disturbance levels the IBI can distinguish.

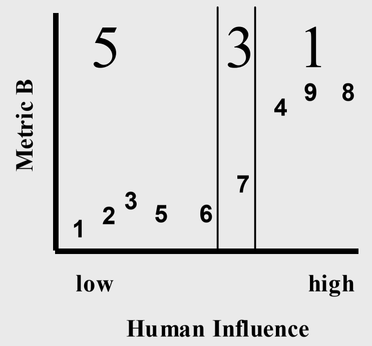
Step 4) Once the IBI is developed, field verification of the proposed scoring system must occur. Classification of new sites based on their level of disturbance is used to predict an IBI, then field studies generate an observed IBI, and the two IBI values are compared.

Perhaps the most critical point to emphasize, IBI's begin with *empirical relationships* derived from monitoring data showing how a group of species in a system responds to varying levels of disturbance. An IBI simply combines a number of these empirical relationships into a standardized, repeatable, and biologically interpretable scoring system. The strength of IBI's is their ability to incorporate many attributes of the biological community into a measurable response to disturbance. For example, many IBI's include multiple functional groups (i.e. ground nesting and cavity nesting birds, terrestrial arthropods, etc), trophic levels (producers, herbivores, meso and top predators), or unique species (native vs. nonnative) to evaluate human disturbance effects on habitats (Karr 1991). As such, a well-developed IBI, which combines response curves from species or taxa each playing different roles in an ecosystem, measures a broad biological response to disturbance. The following figure illustrates the above description.

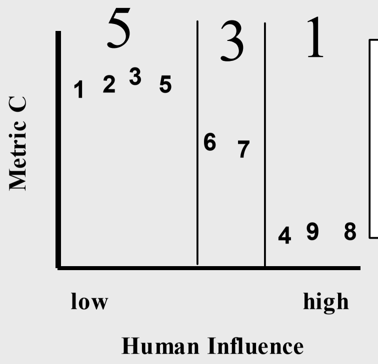
Step 1. 3 response curves. Data for each metric are collected at 8 sites specifically placed so they span a gradient of disturbance.



Metric A shows a linear response to disturbance.



Metric B is useful for separating low from high disturbance.



Metric C shows a sharp, threshold between disturbed and undisturbed sites, with little change within a disturbance category

Step 2. 5, 3, 1 A standard scoring system gives metrics a 5 at low disturbance and a 1 at high, with 3 the intermediate value.

Step 3. Scores for each metric are combined across a site to develop an overall IBI score. Sites are then comparable to each other.

Site	Metric A	Metric B	Metric C	IBI Score
1	5	5	5	**15**
2	5	5	5	**15**
3	5	5	5	**15**
4	1	1	1	**3**
5	5	5	5	**15**
6	3	5	3	**11**
7	3	3	3	**9**
8	1	1	1	**3**
9	1	1	1	**3**

Step 4. Field validation and implementation. After field validation, unknown sites can be sampled and their overall integrity measured relative to the known sites.

The IBI was first developed for fish communities in midwestern streams of the US (Karr 1981, Fausch et al. 1984), and is predominately used to evaluate aquatic ecosystems. Since then, the use of IBI's and sophistication of IBI's has grown primarily on two fronts. The first is the statistical methods used to determine the level of discrimination of a final IBI, which we discuss in our other report (Diffendorfer et al. 2002). The second, which we describe below, is the organizational structure used for creating the guilds, or species for which response curves are derived from monitoring data. We present this methodology here because we report potential guild structures for birds and small mammals, and felt it important to give an overview.

Herricks and Schaffer (1985) presented 6 general criteria for data useful in IBI development. All attempts to build IBI's we have reviewed generally meet these criteria. 1) *The measures used must be biological.* Abiotic responses to disturbance are not included in IBI's. 2) *The measures must be interpretable at several trophic levels, or provide a connection to other organisms not directly involved in the monitoring.* An IBI should measure both composition and function in a system. Thus, IBI metrics should relate to an array of ecological processes. If so, then a change in the index reflects a broader, more complex change in the system. 3) *The measure must be sensitive to the environmental conditions being monitored.* The key point is that the taxa used and the measures chosen (i.e. species richness, abundance, or community overlap, etc) must show true responses to human induced changes of the ecosystem. 4) *The response range (i.e., sensitivity) of the measure must be suitable for the intended application.* In the case of CSS habitat, measures used in an IBI should be able to distinguish healthy CSS from disturbed CSS. If the IBI cannot distinguish disturbed from undisturbed sites, it will not be useful. 5) *The measure must be reproducible and precise within defined and acceptable limits for data collection over space and time.* A measure will be useful to an IBI if, when using a standardized protocol, similar values are generated from repeated samples at the same site. If different samples yield different estimates of the variable being measured, the results are not reproducible and an IBI based on these data would be unreliable. 6) *The variability of the measure(s) must be low*. Any variable used in an IBI will have some inherent level of variability caused by seasonal, temporal, or spatial variation in ecological processes. However, the inherent variability must be significantly less than changes in the variable caused by human disturbance to the ecosystem.

Given these 6 general criteria, the actual variables measured and used in IBI's varies from system to system. Karr and Chu (1999) indicate metric selection is an iterative process, where a specific metric is chosen and then exploratory data analyses used to determine if the metric shows a response curve to disturbance. Karr and Chu (1999, Table 5) recommend four broad categories of metrics for use in and IBI: Taxa richness, Tolerance vs intolerance (e.g. taxa richness of disturbance tolerant vs. intolerant species, etc), trophic structure (e.g. relative number of predators, etc), and individual health (e.g. growth rates, relative abundance of individuals with deformities, etc). More recent IBI's, particularly bird-based IBI's, create "guilds" of species based on rather complex categorization schemes. Generally, 3 broad divisions are initially used (composition, structure, and function) and then more specific categories are derived within each of these categories. We describe this method in the bird section.

Description of task

This deliverable represents the first phase of a multi-year effort. The goal of this phase is to assess our current state of knowledge of CSS food webs and their response to disturbance, and then use this knowledge to design and implement the field studies crucial for developing the species response curves for the IBI. The original contract states this document will review and synthesize scientific and gray literature, as well as expert opinion regarding the response of Coastal Sage Scrub ecosystems to disturbance. In addition, this document was to focus on four items while summarizing the literature and it's relevance to the development of an Index of Biological Integrity: A) identify functional/taxonomic groups or unique species within these groups that are sensitive to human impacts in CSS; B) describe any data gaps regarding how CSS ecosystems respond to human disturbance; C) contain an annotated bibliography for those reference materials that contain valuable information and; D) make recommendations regarding additional areas of research that are needed to better understand how CSS habitat, and the species it supports, respond to human disturbance. Here, and with the attached annotated bibliography (a separate document), we address each of the above points. After discussions with CDF&G, we focused the review on 5 major groups because these groups will likely be included in long-term monitoring plans required by the NCCP process. They include Plants, Birds, Mammals, Arthropods, and Herpetofauna.

Overview of review process, scope of work, and limitations.

General Approach. Dr. Diffendorfer oversaw the literature review and synthesis while graduate students and a post-doctoral researcher (Dr. Rosalie del Rosario) performed the majority of the work. Graduate students only worked on taxa for which they had expertise. They interacted closely with Dr. Rosario to screen articles and reports. Students met with Dr. Diffendorfer bi-weekly to discuss the progress of the reviews and key publications from March - December, 2001. The entire research group met weekly to discuss key papers, drafts of taxa reviews, and the scope of the project. Each graduate student wrote the initial review for a taxa. This draft was then edited by the Drs. Diffendorfer and Rosario and reviewed by the entire group. The considerable experience of the graduate students is summarized below.

Vegetation: Genie Flemming, MS student. Ms. Fleming has been involved with ecological research for over 6 years and has extensive experience working in coastal sage scrub and a variety of other plant communities in S. CA and elsewhere. Since 1995, Ms. Fleming has been employed with Dr. Paul Zedler as a research assistant, and has been responsible for collection of field data, plant identification, data management, and writing project reports. Dr. Zedler's lab has conducted several research projects, including long-term vegetation trend monitoring on Marine Corps Base Camp Pendleton. This project is primarily concerned with investigating the responses of vegetation communities on the Base, including CSS, to major disturbances associated with military training activities. Other projects include measuring the response of riparian vegetation to changes in groundwater, long-term ecological monitoring on Twenty Nine Palms Marine Corps Base, and monitoring populations of rare or sensitive plant species such as *Pinus torreyana*, *Cupressus forbesii*, *Brodiaea filifolia*, and *Dudleya multicaulis*. In addition, Ms. Fleming worked on a multi-taxa research project conducted by Dr. Guy McPherson and Dr. Bob Steidl at the University of Arizona from September 1999 until October 2000. This project investigated the responses of both the flora and fauna of semiarid grassland to varied fire regimes. These experiences have provided Ms. Fleming with a strong understanding of plant community ecology and, in particular, the responses of communities to anthropogenic disturbance.

Mammals: Jenny Duggan, MS. Student. Jennifer Duggan attended the University of Wisconsin-Madison as an undergraduate and earned Bachelors degrees in both zoology and psychology. Since entering the Masters program in Ecology at SDSU under the advisorship of Dr. Diffendorfer, she has handled thousands of small mammals belonging to 18 species found throughout S. CA. Ms. Duggan is currently involved in a variety of local ecological projects, including her thesis research (The effects of food supplementation on small mammal communities over chaparral-grassland ecotones), surveys with USGS, and surveys with the U.S. Fish and Wildlife Service for the endangered Pacific Pocket Mouse. Her thesis work has given her considerable experience in the S. CA small mammal literature as well as an in-depth background in mammalian population and community ecology.

Avifauna: Robert Chapman, MS student. Mr. Chapman has been involved with birding for more than 20 years in California, Arizona, and Nevada. His background as an electronics engineer provides him with mathematical and analytic tools and skills that fit nicely into ecological studies of birds in a variety of habitats. His field experience includes working with the Yellow-billed Cuckoo and with the Global Climate Change team in Alaska. He has mist netting, banding, and survey experience. His Masters program work will apply GIS techniques and spatial analysis tools to the use of avifauna as indicators of habitat health.

Herpetofauna: Milan Mitrovitch, Ph.D Student.

Arthropods: Matthew Rahn, Ph.D Student. Mr. Rahn's Ph.d focuses on the ecological assessment of ground obligate beetle diversity in CSS and their response to anthropogenic disturbance. He has extensive experience in arthropod ecological research, community ecology, and large-scale habitat conservation planning and monitoring. He investigated patterns of bat community assemblage and it's application to the Clark County, Nevada HCP for his MS. He has published work on arthropod community structure on isolated dune habitats in the Great Basin and has been conducting field research on terrestrial arthropods since 1994. Most recently he has been working on a review of various Habitat Conservation Plans and their inventory/monitoring plans across a range of taxonomic groups.

Scope of work. We reviewed published material to help us understand how different species or taxa in CSS respond to anthropogenic impacts (see a list of disturbances below). Because few studies were designed to directly assess a particular species' or communities' response to a particular form of disturbance, we "cast a broad net" when selecting material to review. We reasoned a broader approach may 1) reveal information which, while not directly showing responses to disturbance, could lead to hypotheses about possible responses, and 2) help develop a mechanistic understanding regarding observed responses to disturbance or predict how these responses may impact other taxa in CSS. For example, papers showing habitat preferences of CSS birds, diets of rodents, or indirect evidence for trophic cascades between top predators, mesopredators, birds and small mammals, were reviewed, as well as publications reporting more direct responses of CSS taxa to disturbance.

Disturbance. We defined disturbance as any human-caused factor potentially affecting the integrity of CSS. The following variables were considered disturbances. Fire, Grazing, Edge, Roads, Mechanical disturbance, Agriculture, Air pollution, Light pollution, Habitat Fragmentation, and Recreation. In each case the impact on CSS will depend on the intensity, time since, history of, frequency, and size of the disturbance. We recognize the presence of any one type of disturbance is likely correlated with many of the other disturbance types, making it difficult to easily separate effects of each form of disturbance. For example, urban sprawl likely increases the incidence of all of the forms of disturbance in a given area except grazing and agriculture. Given these complexities, it was impossible, based on the literature review, to ascertain the unique effect of each disturbance type on particular taxa. When possible, we noted the responses of CSS taxa to those unique forms of disturbance studied.

The reviews. In general, publications were found by searching library databases, including government document searches, asking local experts for papers, and general Internet searches. Publications with potentially interesting titles were scanned and read further if they contained pertinent information. Bibliographies of pertinent papers were researched in detail to check the original sources of information. As publications were gathered, they were categorized as follows. The annotated bibliography contains papers in categories A and B. We chose to limit the bibliography to those papers focusing on responses to disturbance in CSS, because CDF&G already has an extensive bibliography on the ecology and natural history of CSS provided by Dr. John O' Leary, San Diego State University.

A) Critical paper: Papers specifically addressing the goals of the review and/or show responses of CSS taxa to disturbance. These often included specific studies of a species or taxa's response to a specific disturbance type.
B) The study focused specifically on responses to disturbance but did not carry the significance of critical papers. This may be due to experimental flaws, small sample sizes, a lack of a relationship, or that the work was carried out in habitat similar, but different from CSS (i.e. chaparral, or Mediterranean scrub habitat).
C) The study was not designed to specifically study responses of CSS to disturbance, but information regarding CSS response to disturbance could be extrapolated from the findings.
D) The publication was not focused on CSS and disturbance, but does give pertinent information on the natural history of CSS.

Taxa reviews. The depth of any given taxa review depended solely on the level of past research, which was highly variable. For example, the literature on CSS vegetation is enormous, with large reviews and bibliographies already in place, including one funded by California Department of Fish and Game (i.e. at http://www.ceres.ca.gov/CRA/NCCP/). In stark contrast, only a handful of papers have been published on both arthropods and mammals in CSS and even fewer on how these taxa respond to disturbance. Birds, like vegetation, are reasonably well studied. Finally, our review of the herpetofauna is somewhat terse. We choose not to emphasize this taxa given the tremendous amount of research and data collected by Dr. Robert Fisher (USGS). Dr. Fisher's data, as it is analyzed over the next 1-5 years, will quickly outdate any historic information we may have discovered. Nonetheless, we make some interesting observations about the herpetofauna, which we hope are evaluated using Dr. Fisher's data. Overall then, the structure of each taxa review is quite different, emphasizing different key points illustrated by past research. We conclude each taxa review with a section entitled "Data gaps and recommendations for future research."

Limitations. As with any literature review and synthesis, this review has limitations. The most obvious limitation is simply the rarity of research in CSS. The exception to this point is vegetation, where a large literature exists primarily on responses to fire. In general, studies on many of the animal taxa in CSS are limited in number and only a few specifically address responses to disturbance. As such, conclusions from this review should be viewed as working hypotheses. Second, scientific literature, especially when gray literature is included, is vast and difficult to completely cover. As such, we may have missed relevant publications. We attempted to minimize this by doing a thorough review, and we feel the vast majority of publications available through numerous digital databases were covered. However, obscure reports by local consultants or academics to government agencies are likely missing. Finally, we would like additional expert opinion and consider this current deliverable a work in progress. We realize scientists bring their own unique knowledge, experience and bias to a specific issue. We interacted with some individuals but not all, and feel this document could evolve with additional peer review.

Results

Vegetation

Introduction

Facultatively drought-deciduous and seasonally dimorphic shrubs dominate the vegetation community, along with stem and leaf succulents in some areas. The community is also characterized by an herbaceous “understory” consisting of perennial and annual grasses and forbs within the open spaces between shrubs. The distribution of CSS extends from San Francisco, CA south to El Rosario, Baja California (Kirkpatrick and Hutchinson 1977, Westman 1981a, O'Leary 1990a, DeSimone and Burk 1992), and the community is found on coastal plains and foothills of the Transverse and Peninsular Ranges and on the California Channel Islands (Westman 1981, O'Leary 1990). South of San Diego, CA succulents become much more common, and the community may be differentiated as coastal sage-succulent scrub (Mooney 1988). Species composition is highly variable at both local and regional scales, and several floristic associations and subassociations within the community have been described (Kirkpatrick and Hutchinson 1977, Axlerod 1978, Westman 1981a, DeSimone and Burk 1992). In southern California, common shrub species occurring as dominants or co-dominants in stands of CSS include *Artemisia californica* (California sagebrush), *Eriogonum fasciculatum* (California buckwheat), *Encelia californica* (brittlebush), *Salvia mellifera* (black sage), and *Salvia apiana* (white sage). Some stands may also include hard-leaved, evergreen shrubs, such as *Malosma laurina* (laurel sumac) and *Rhus integrifolia* (lemonadeberry), though dominance by such shrubs is more characteristic of chaparral vegetation with which CSS sometimes intergrades. Local species composition and shrub cover are likely influenced by local climate, substrate, and other environmental variables (Westman 1981a, DeSimone and Burk 1992), as well as by disturbance (Kirkpatrick and Hutchinson 1980).

The dominant plants of the CSS vegetation community have traits allowing rapid post-disturbance recovery. Thus, the community as a whole exhibits resilience to some disturbances. Axelrod (1978) argued the current distribution of CSS is due, in part, to anthropogenic disturbance regimes having converted grassland and chaparral to CSS. This suggests the CSS community may be disturbance dependent or successional in nature. In some areas, CSS may, in fact, represent a successional stage. CSS species often temporarily occupy recently burned chaparral sites. Possibly because the drought-deciduous, small-leaved CSS shrubs better tolerate the drier site conditions following fire (Westman 1982). Nonetheless, stable CSS communities are known to exist in undisturbed sites (e.g. Westman 1982). These climax CSS communities are typically found at lower elevations and/or more xeric sites than areas tolerated by chaparral (Westman 1981b, 1982, Mooney 1988) and with soils more basic, shallow, and rocky than those found in native perennial grasslands (Keeley 1993).

While we are primarily concerned with CSS as a climax community, the successional nature of CSS may present difficulties for defining the vegetation type at a specific site. In particular, as will be discussed in greater detail below, a few CSS shrub species often become established on disturbed areas such as road cuts or firebreaks within other vegetation communities (Zedler 1981, Davis 1994, Zink et al. 1995). While these shrubs may dominate the disturbed site for some time, it is not clear how long they persist in the absence of repeated disturbance. In addition, it is not clear other elements of the CSS community, such as native herbs or faunal associates, establish along with these shrubs. Thus, such vegetation is probably best not considered “true” CSS, but it may closely resemble disturbed CSS. If the two types of vegetation are, indeed, very similar, it may not be possible using an IBI alone to distinguish degraded CSS habitat from degraded areas where CSS elements have invaded. However, additional site characteristics and historical land records can be consulted as necessary to aid in restoration efforts and other management decisions when vegetation history is in question.

Disturbance Effects on Coastal Sage Scrub Vegetation

A variety of disturbance types, both historic and ongoing, impact the CSS community throughout its range. Perhaps the most studied of these disturbances is fire. Fire is a natural disturbance in CSS and one to which the community is adapted. Yet, as urbanization around natural areas increases the incidence of fire in shrublands also increases (Keeley et al. 1999). Thus, atypically high fire frequencies could pose a threat to the vegetation community. Other common disturbances, such as grazing and mechanical disturbance, are similar to fire because they remove or physically damage aboveground vegetation, but differ enough to expect alternate community responses. Grazing has occurred in California shrublands since European settlement, but is not as well studied in CSS as in other vegetation types. Mechanical disturbances may be associated with increased urbanization or recreation in wildland areas and include temporary land clearing and vehicle or heavy foot traffic. Less obvious disturbances include damage to plant populations by increased air pollution and habitat fragmentation. The evidence of these latter disturbance types may take longer to appear, but the disturbances still may result in dramatic changes to the community over time.

Here we review the response of CSS vegetation to the disturbances listed above. In some cases, we include literature regarding similar mediterranean-type plant communities, such as chaparral, because few studies have documented the effects of some specific disturbances in CSS. Ultimately, the specific response of CSS vegetation on any given site to any given disturbance may vary due to a variety of factors. However, some consistent response patterns do appear. In particular, as disturbance becomes more frequent or more severe, the abundance of exotic plant species, particularly annual grasses and forbs, increases. While reporting this trend may not be novel, focusing on it may, nonetheless, be useful. Exotic plant invasions may, themselves, represent a type of disturbance, and an abundance of exotic species within a stand of CSS vegetation may indicate that critical community processes have been disrupted by past disturbances and subsequent invasion. If the abundance of exotic species can be shown to serve as an indicator of past disturbance and a partial indicator of present ecosystem health, it may serve as a useful tool for land managers designing plans for habitat recovery or preservation.

Fire

Periodic fire is common in mediterranean-type shrublands like CSS and may be viewed as a natural, or even necessary, disturbance. Many shrubs and herbs in CSS recover rapidly after fire and are, therefore, considered “fire-adapted”. Most notably, common CSS shrub species, as well as some perennial forbs and grasses, resprout from underground rootstocks or re-establish from seeds in the soil. Some “fire-following” annual species require special germination cues provided by fire, and are only visibly present in the first few years after a site has burned (Keeley and Keeley 1984, O'Leary and Westman 1988). Whether or not the various recovery mechanisms involved are adaptations to fire specifically is debatable (see White 1995). Nevertheless, these mechanisms impart resilience to CSS in the event of fire. There are, however, limits to this resilience as fire becomes more frequent (Zedler 1995).

The fire ecology of chaparral vegetation has been studied more extensively than that of CSS. Yet, literature from both vegetation communities provides important information regarding post-fire recovery of shrubs and herbaceous plants found in CSS, as well as providing estimates of a natural fire regime. Much of the literature concerning post-fire recovery of CSS vegetation has been reviewed by O'Leary (1990a) and White (1995) and is briefly summarized below.

Just as the pre-fire species composition of CSS varies with environmental variables (Westman 1981a), post-fire recovery patterns are highly variable in CSS and depend on factors such as geographic location (e.g. coastal vs. inland sites), slope aspect, season of burn, and fire intensity (Westman 1981b, Keeley and Keeley 1984, O'Leary 1988, O'Leary and Westman 1988, O'Leary 1990b). More research is needed, however, to determine if and how these variables consistently affect post-fire species composition and recovery. In areas closer to the coast, resprouting is generally more important for most CSS shrub species than seedling recruitment, but resprouting shrubs often seed abundantly during the first post-fire year (Keeley and Keeley 1984, O'Leary and Westman 1988). At sites further inland, however, resprout rates of shrubs following fire are lower than in coastal areas, so that re-establishment from seed is important (O'Leary and Westman 1988). CSS shrubs and subshrubs may recover half or more of their pre-fire density and cover within 5 to 7 years after fire, though inland sites may take longer to recover (Westman 1981b, O'Leary and Westman 1988).

The cover of herbaceous plants (i.e. forbs and grasses) is generally high following fire and declines as shrub cover increases (Westman 1981b, Keeley and Keeley 1984, O'Leary 1990b). In CSS, herbaceous cover generally remains higher than in chaparral long after fire due to the more open canopy of the CSS plant community (O'Leary 1990a). Plant species diversity (e.g. species richness and equitability) in CSS is often highest in the first few years after fire, primarily due to the diversity of herb species which include some fire-following species (Westman 1981b, Keeley and Keeley 1984, O'Leary 1990b). Post-fire declines in diversity have been found to differ according to slope aspect, such that north facing slopes may retain higher herb richness, equitability, and cover for quite some time compared to south facing slopes (O'Leary 1990b). Though both herbaceous cover and diversity generally decline after the first few post-fire years, a second temporary peak may occur after 20 years with the appearance of a different suite of herbs than those seen immediately post-fire (Westman 1981b).

Natural, or pre-European, fire return intervals for CSS are unknown, and estimates of average fire return times within the last century are highly variable. Westman (1982) reported an average fire return time of 20 years in CSS in the western Santa Monica Mountains based on fire data from 1930 to 1978. Minnich (1983, Table 2) presented data for fires between 1972 and 1980 implying an average fire return time of over 100 years in CSS in southern California. Keeley et al. (1999) compiled fire data from several shrubland-dominated California counties and calculated fire return intervals prior to 1951 and after 1950. While return intervals varied substantially among counties both prior to and following the mid 1900s, fire return intervals decreased in all but 2 counties after 1950, suggesting natural return intervals may have been longer than those seen currently. Though the abundance of herbaceous vegetation in CSS contributes to fuel accumulation and the ability of the community to carry fire over relatively short intervals, additional evidence supporting long natural intervals comes from the low occurrence of lightning-caused fires in coastal areas where most CSS occurs (Keeley 1982), suggesting natural rates of ignition in CSS are low. If fire is necessary at some interval to maintain the CSS vegetation community, it is not clear what interval is ideal or how variability in fire return time affects the community. Many shrubs may be capable of surviving long fire-free intervals (Malanson and Westman 1985, Zedler 1995), but little is known about the seed bank longevity of fire-following annuals that occur in the CSS understory.

In the absence of fire over long intervals, the stability of the CSS shrub community varies. For example, where fire and other disturbances have been absent for 60 years or more, some stands of CSS in central California have been at least partially replaced by chaparral on south facing slopes or oak woodland on north facing slopes (Callaway and Davis 1993). However, structurally intact stands of CSS that have not burned in over 60 years are known to exist (Westman 1982). In essence, CSS appears to be a successional stage on some sites, but climax vegetation on others. Where CSS exists as a successional stage, shorter than natural fire return intervals might arrest successional progress towards the true climax and favor persistence of the CSS vegetation. Stability of CSS vegetation as a climax community in the absence of fire is likely related to environmental factors at a given site and to the ability of CSS shrubs to produce new basal shoots continually without fire (Malanson and Westman 1985). In addition, some CSS shrub species are able to recruit seedlings between fires, though this recruitment may be dependent on small mammal consumption of herbaceous vegetation in the stand, which provides suitable gaps for seedling establishment (DeSimone and Zedler 1999). Although overall plant species diversity may decline over time in unburned CSS, other late-successional taxa, such as some lichens, may require mature, undisturbed CSS communities for population expansion (Bowler and Riefner 2000). Thus long fire return intervals do not appear obviously detrimental to the CSS community, and some have suggested that long intervals are probably better than shorter ones (Keeley 1995, Zedler 1995).

Short fire return intervals, or increased fire frequency, in CSS appear more likely to dramatically change community composition or cause vegetation type conversion than long fire intervals. Though CSS may be more resilient to repeated fire than chaparral (Kirkpatrick and Hutchinson 1980, Keeley and Keeley 1984, O'Leary 1990a), frequent burning over short time intervals can eliminate or reduce some shrub and subshrub species such as *Eriogonum fasciculatum* (Zedler et al. 1983), *Salvia mellifera* (Haidinger and Keeley 1993b) and *Lotus scoparius* (California broom, deerweed) (Zedler et al. 1983, Haidinger and Keeley 1993a). Burning has also been associated with an increased transition rate from CSS to grassland (Callaway and Davis 1993). The transition of shrubland to grassland may involve not only direct damage to native shrub populations by fire, but also the invasion of shrublands by exotic annual grasses and forbs. These exotics may be favored by frequent fire, may further decrease the fire return interval by increasing fuel loading and continuity, and may also inhibit germination and/or survival of shrub seedlings. Haidinger and Keeley (1993a) compared chaparral sites with 1, 2, or 3 burns in a six year period and found the density and percent composition of non-native annuals increased while species richness and percent composition of natives decreased with increased fire frequency. The exotic annuals were, in contrast, absent or present in low abundance on sites with only one burn over a 20-year period. Similarly, Giessow (1997) found abundance of exotic grasses and forbs and exotic forb richness were positively correlated with fire frequency in CSS. The increased abundance of exotic annuals not only increases chances for a repeat fire over a short interval (Zedler et al. 1983, D'Antonio and Vitousek 1992), but the exotics may compete with native shrub seedlings for critical resources such as soil moisture (Eliason and Allen 1997). Thus, increases in exotic species may inhibit shrub recovery after fire especially at sites where recruitment from seed is important.

While frequent burning may facilitate type conversion of shrubland to a landscape dominated by exotic plants, repeated burning may not always be necessary. A single fire may provide the opening needed for aggressive invaders and may result in more rapid vegetation type conversion. For example, Zedler (1988) found that *Carpobrotus edulis* (ice plant, fig marigold) was able to invade chaparral after a single controlled burn and had the second highest cover of any perennial plant 3 years after the fire. Prior to the fire, *C. edulis* was only known to be present on the disturbed edges of the chaparral stands. As noted by the author, this illustrates the importance of edge effects in determining community response to disturbance.

More research is needed regarding the effects of varying fire histories on CSS vegetation. It appears, however, that very short fire return intervals negatively impact the vegetation community. In particular, increased fire frequency generally decreases abundance of some native shrubs, increases the abundance of exotic plant species, and may result in conversion of CSS into exotic annual grassland. The frequency of fire necessary to result in such a conversion has been estimated as a return interval of less than 5-10 years (see O'Leary 1990a), but will likely vary with the pre-burn condition of the CSS community, the size of the stand (or patch size), and the species composition of stand edges. Presence of exotic plants within the stand prior to burning, small patch sizes, and edges with an abundance of exotic species will all likely increase the potential for and rate of CSS conversion following fire.

Grazing

Grazing has been a common and, in some cases, intense disturbance in many southern California plant communities since the arrival of the early European settlers (Dodge 1975). In general, studies across a variety of plant communities reveals grazing damages perennial grasses and forbs through removal of aboveground biomass, but may also stimulate or enhance production of new growth (e.g. Menke 1992) and provide openings for new seedling establishment. Shrubs and small trees may be damaged both by direct browsing and trampling by grazers. Grazing can also increase soil erosion and compaction, and grazers may directly introduce propagules of exotic species into the areas where they graze (Clark 1956, Groves 1986). Though many publications report the effects of grazing in grasslands, very few studies have examined the direct effects of grazing on CSS. Nonetheless, competing theories regarding the effects of grazing on CSS have emerged. On the one hand, it is possible that grazing may benefit CSS and may have contributed to expansion of the vegetation community historically. Alternatively, heavy grazing may be responsible for the conversion of CSS into grassland dominated by exotic annual plants.

While not addressing the direct effects of grazing within CSS specifically, some evidence suggests that grazing might facilitate the persistence or expansion of CSS shrubs. By comparing disturbance history with vegetation changes derived from aerial photos acquired in 1947 and 1989, Callaway and Davis (1993) found grazing slowed the rate of transition from CSS to chaparral. This could indicate that grazing, like fire, might help maintain the CSS community in some circumstances. Others have suggested grazing actually promotes CSS expansion by asserting that historic overgrazing accounts, in part, for the current geographic distribution of CSS. Dodge (1975) and, to a lesser extent, Kirkpatrick and Hutchinson (1980) argued heavy grazing following introduction of livestock by Spanish settlers allowed shrub invasion into grasslands by reducing competition from grasses and by reducing fuels and fire frequency in grasslands. Axelrod (1978) added that overgrazing resulted in erosion of the soils that support grasses, which also facilitated the expansion of CSS into grassland.

Strong evidence for expansion of CSS or chaparral since European settlement is lacking, however. Mensing (1998) analyzed pollen cores from 2 sites near Santa Barbara and found only a slight (~2-3%) increase in *Artemisia* pollen since 1820 and no consistent trends in pollen percentages of chaparral-type species, thus providing weak or no support for theories suggesting a grazing-related increase in mediterranean-type shrubland. In addition, some studies indicate that grazing does not facilitate expansion of CSS into grassland. For example, Callaway and Davis (1993) showed both fire and grazing in grasslands limited invasion by CSS species. McBride (1974) reported replacement of grassland by *Baccharis pilularis* (chaparral broom, coyote brush) scrub after livestock grazing had been eliminated, but actively grazed grasslands were relatively free of shrubs, and cattle were observed foraging on shrub seedlings. Similarly, examination of transition zones between CSS and grassland in grazed areas by Freudenberger et al. (1987) revealed that shrub seedlings were largely absent outside of CSS stands indicating shrubs were not invading the grassland.

Oberbauer (1978) pointed out that theories of grazing-facilitated shrub expansion into grassland are, to some extent, based on the expansion of some spiny and unpalatable shrubs into grazed desert grasslands. Most CSS shrubs lack such defenses and are more likely damaged by grazing as observed by McBride (1974). Thus, it may be more likely that grazing facilitates expansion of grassland vegetation into CSS. Oberbauer (1978) reported a decline in CSS and expansion of grassland between 1928 and 1975 in part of San Diego County that may have been related to grazing. Similarly, Freudenberger et al. (1987) found an overall increase in grasslands "at the expense of coastal sage scrub and chaparral" (p. 15) between 1928 and 1980 in the Los Angeles basin where grazing has been widespread. In the transition zones between grassland and CSS examined by Freudenberger et al. (1987), soils of grasslands near transitions were more similar to those within CSS than to other grassland soils. Based, in part, on this type of evidence, some authors (e.g. Keeley 1993, Hamilton 1997) now reject the notion of widespread native grasslands in parts of California prior to European settlement, and argue instead that many present-day exotic annual grasslands were historically CSS and chaparral degraded by disturbances such as frequent fire and overgrazing.

Studies on the California Channel Islands, where grazing by domestic and feral animals has been intense and widespread, provide additional evidence that heavy grazing may promote conversion of CSS to exotic grassland. These studies show grazing damages mature shrubs, as well as seedlings, and creates patches of bare ground, both of which might facilitate invasion by exotic plant species. Coblentz (1980) compared areas on Santa Catalina Island with feral goats to areas where goats were extirpated 15 years previously. He found elimination of sagebrush and reduction of total vegetative cover by ~40% in goat inhabited areas. Van Vuren and Coblentz (1987) studied grazing by feral sheep on Santa Cruz Island and found the animals foraged on native shrubs late in the growing season after most herbs had dried. Sheep browsing partially defoliated large chaparral shrubs, completely defoliated low growing shrubs such as those found in CSS, and reduced shrub regeneration. In addition, sheep grazing was associated with reduced herbaceous cover and increased bare ground. Many of the common exotic grasses and forbs in California are fast-growing, disturbance-adapted species (Oberbauer 1978, Groves 1986) that may be well equipped to exploit the openings created by grazing so that vegetation type conversion could eventually result. Indeed, landscapes of the California Channel Islands are often dominated by exotic grasses, and a comparison of historical photographs with present-day vegetation on Santa Catalina Island showed areas previously covered by chaparral and CSS were covered largely by grass and only scattered, large shrubs after decades of grazing (Minnich 1982).

Although grazing by feral animals may be more destructive than domestic livestock grazing (Coblentz 1980), the studies above provide insight into the potential relationship between heavy grazing, exotic species invasion, and vegetation-type conversion in CSS. There is also some evidence that less intense grazing increases the abundance of exotic plant species in CSS and that these exotics may become persistent components of the vegetation. In a study of CSS composition across the Channel Islands, (Westman 1983) found grazing was associated with an increase in the abundance of exotic species, even though he attempted to minimize the effects of grazing in his study and many areas had not been grazed in several years. The low levels of grazing in his study areas did not affect the distribution of dominant CSS species relative to other biogeographic factors suggesting that the dominant CSS shrubs may be able to tolerate or recover from light grazing. However, stands of CSS on the inner Channel Islands had a higher percentage composition of exotic species compared to mainland sites, which as a whole had a less intense grazing history than island sites. Westman (1983) suggested this was due to increased colonization by exotics on the islands following reduced shrub cover associated with grazing. Similarly, O'Leary and Westman (1988) reported a higher proportion of exotic species in CSS at inland sites where grazing pressures were higher compared to coastal sites.

The studies reviewed above suggest grazing can damage CSS shrubs and reduce overall plant cover, and intense grazing may result in conversion of CSS to exotic grassland. The level of intensity required for such a conversion, and whether such a conversion is permanent, is unclear. (McBride 1974) found that shrubs reinvaded grasslands after grazing was eliminated, and other studies (Oberbauer 1978, Freudenberger et al. 1987) found evidence of shrub succession in grasslands where some grazing was known to occur. Even without permanent vegetation-type conversion, however, grazing does appear to be associated with the invasion of CSS by exotic plant species, and these exotics may persist as permanent components of the vegetation after shrubs have recovered from grazing.

Mechanical Disturbance

We define "mechanical disturbance" as disturbances resulting in damage to, or complete destruction of, aboveground vegetation by mechanical means. This includes intentional clearing or crushing of vegetation with heavy machinery or vehicles, as well as human foot traffic, which results in similar, though typically less intense, damage. Mechanical disturbances may occur as a result of urban and suburban development, agriculture, road and fuel break construction, or recreation and, in all cases, covers a range of intensities. Like grazing, mechanical disturbances may not only directly damage plants, but may increase soil erosion and compaction. In addition, the vectors of mechanical disturbance, like livestock, can introduce non-native vegetation into the disturbed area, and the openings created by the disturbance may provide the opportunity for exotic plant establishment. Although there are several potential sources and consequences of mechanical disturbance in CSS, few studies detailing the effects have been published.

A small number of studies suggest CSS can recover from even intense mechanical disturbance over time. Narog et al. (2000) examined recovery of an artificially created stand of CSS shrubs subjected to mechanical removal of all aboveground vegetation. The stand was originally planted with *Artemisia californica, Eriogonum fasciculatum, Encelia farinosa, Salvia mellifera*, and *S. apiana* in equal numbers maintained by seedling removal and replacement of dead plants prior to the disturbance. Four years after the mechanical disturbance, all shrub species had re-established on the site from both resprouting individuals and seedling recruitment and had "increased in number and density over time"(p. 265). *A. californica* and *E. fasciculatum* were the most abundant shrub species (56.8 and 29.5 percent, respectively) four years after the disturbance primarily due to successful seedling establishment. Similarly, Westman (1976) found native shrubs re-established in an area bulldozed and planted with exotic species 13 years earlier in a fuel control effort. *A. californica* dominated the site, again due to seedling establishment, despite its low representation prior to disturbance. In both studies, some supplemental water was provided after the disturbance and may have contributed to successful re-establishment of native species. In fact, Westman (1976) showed both irrigation and fertilizer addition generally enhanced reinvasion and increases in cover by native species.

The relative success of *A. californica* and *E. fasciculatum* by seedling recruitment suggests these species may be better able to invade openings created by mechanical disturbance and, thus, may be more resilient to some disturbances than other CSS shrubs. In fact, these species are well-known colonizers of disturbed areas such as road cuts and old fields within a variety of vegetation communities (Zedler 1981, Davis 1994). The lightweight, wind-dispersed seeds of these shrub species may allow for rapid colonization of disturbance-related gaps suitable for germination and seedling establishment. While additional evidence for the resilience of these and some other shrub species can be found (Davis 1994, Zink et al. 1995), resilience of these species within a CSS community does not guarantee recovery of the community as a whole. Other studies have shown a failure of CSS plant community recovery following mechanical disturbance.

Zink et al. (1995) studied recovery of vegetation on a mechanical disturbance corridor created by underground pipeline construction through a nature reserve. The construction affected four major plant communities: grassland, CSS, chaparral, and oak woodland. After the disturbance, the construction site was seeded with a mixture of native and exotic species. A survey of the site more than 10 years after the disturbance revealed *E. fasciculatum* and *A. californica* successfully re-established along all or most of the disturbance corridor. Overall native shrub cover did not significantly differ between disturbed sites within CSS and adjacent, undisturbed CSS, but disturbed CSS showed greater similarity to other disturbed vegetation communities than to undisturbed CSS. Exotic species had significantly higher cover, and native herbs had significantly lower cover in all disturbed communities compared to undisturbed vegetation. While direct seeding of exotics following construction may have aided in the establishment of some species, the most abundant exotics at the time of the survey were annual grasses not included in the original seed mix. These exotics were present in areas surrounding the reserve. The abundance of these grasses more than 10 years after the disturbance suggests they were able to successfully invade following disturbance and might be persistent components of the post-disturbance community. Davis (1994) noted a similar increase in and persistence of exotic species in mechanically disturbed CSS. Comparison of a chronosequence of relatively undisturbed CSS and chaparral with near-by shrublands that had experienced severe mechanical disturbance between 2 to 71 years previously revealed greater exotic species richness and percent cover of exotic forbs on disturbed plots. While *E. fasciculatum* and *Baccharis sarothroides* (broom baccharis) were present on disturbed sites, shrub cover and richness of native forbs were greater on undisturbed plots. In addition, there was no correlation between time since disturbance and percent similarity between disturbed and undisturbed plots nor was there evidence of increases in shrub cover or decreases in exotic cover as disturbed sites aged.

The studies by Zink et al. (1995) and Davis (1994) suggest intense mechanical disturbance, like frequent fire and grazing, is associated with a significant, and possibly permanent, increase in exotic plant species abundance and decrease in native herbs on disturbed sites. Zink et al. (1995) further argued that localized persistence of exotic species on disturbed sites may facilitate invasion into adjacent undisturbed areas. Work by Giessow (1997) provides some evidence for facilitated invasion. He examined the impacts of firebreaks on exotic species abundance and richness in CSS. While no overall difference was found between plots with and without firebreaks, within plots located adjacent to firebreaks exotic plant biomass was higher at locations closer to (0-10m) firebreaks than farther away. In addition, 8 of the 27 non-native species present at the study sites were only found at sites near firebreaks. This implies that the presence of firebreaks, or similarly intense, localized disturbances, may be an important contributing factor to some exotic species invasions. In other words, some exotic species may be dependent on disturbance to invade new sites. Relatively localized disturbances, such as firebreak construction and other mechanical disturbances, may allow introduction of exotics into otherwise undisturbed sites. Subsequent large-scale disturbances, such as fire, may then allow proliferation of the exotics further from the site of introduction. Mechanical disturbance might also affect the abundance or composition of plant predators (herbivores and granivores) which might, in turn, affect the relative abundance of native versus exotic plants in the disturbed area and the subsequent dispersal of these species (Giessow 1997).

The studies above illustrate that some CSS shrubs possess the ability to recover from mechanical disturbances via the same mechanisms seen in post-fire recovery. While resilience of these shrubs may aid post-disturbance recovery, changes in local shrub species composition may result due to differential resilience among CSS shrub species. Yet, given the overall variability in CSS shrub species composition and its strong relationship to soil and climate variables, it could be difficult without preexisting data to determine whether shrub species composition on any given site is primarily a function of disturbance history or environmental variables (Zedler 1981). However, studies also suggest mechanical disturbance increases the potential for exotic species colonization and spread, and that exotics may persist as evidence of disturbance even after shrubs recover. The low cover and richness of native herbs noted on mechanically disturbed sites indicates that these community components may be directly affected by disturbance or that exotic species may replace the native herbs and interfere with overall community recovery over time.

Air Pollution

Increasing urbanization and industrialization often result in increases in atmospheric pollutants such as ozone, sulfur dioxide, and oxides of nitrogen. Some of these pollutants have harmful effects on plant tissues, but documenting the direct effects of pollutants on natural plant communities is difficult given time lags in response to pollution and the high number of potentially confounding variables in natural systems. Nonetheless, studies show high levels of pollutants are correlated with decreases in cover of native shrubs and increases in exotic plant abundance in CSS.

In the southeastern Riverside basin, air pollution concentrations are often higher than elsewhere in southern California, and may play a role in the successional and floristic differences seen between CSS in this region and low pollution regions (Westman 1979, 1981b, O'Leary and Westman 1988). Westman (1979) used correlation and path analysis of data collected from 67 southern California CSS sites to determine potential causes of reduced cover of native plant species in certain sites. Analyses suggested that, of the 43 variables included, increases in the mean annual concentration of oxidants was the most likely causal factor relating to decreased cover of natives. Increased oxidant levels were also related to decreased species richness and equitability (Westman 1979, 1981b). Studies have also shown that CSS in the Riverside basin has a high cover of exotic species compared to other sites, and factors associated with air pollution have been suggested as a potential cause of increased exotic species abundance (Westman 1981b, Westman 1981c, O'Leary and Westman 1988, Allen et al. 1997, Minnich and Dezzani 1998). O'Leary and Westman (1988) hypothesized that pollution damage to perennial CSS species resulting in decreased growth and resprouting ability and presence of pollution resistant strains of exotics such as *Bromus madritensis ssp. rubens* (red brome) may explain the species composition in high pollution areas.

The above studies are largely correlational in nature and, thus, do not effectively separate the effects of atmospheric pollutants from the effects of other disturbances, such as frequent fire and grazing, which are also common in the Riverside basin (see Haidinger and Keeley 1993a). Some studies have attempted to isolate the effects of various pollutants on the CSS community, however. Preston (1988) examined the effects of sulphur dioxide (SO_2) emissions from an oil refinery on stands of CSS, focusing particularly on the physiologic and growth changes in the dominant shrub *Salvia mellifera*. Sites along an SO_2 gradient downwind of the refinery were compared with stands in relatively pollution-free upwind sites. Stomatal resistance, intranodal stem length, and heights of Salvia shrubs were reduced in the downwind, polluted sites compared to upwind sites, though no significant trends were found along the downwind pollution gradient. Decreased perennial cover, increased defoliation and reduced leaf size of Salvia, and increased exotic species cover were also found in the most polluted sites close to and downwind of the refinery compared to sites further away or upwind.

While these results suggest high levels of SO_2 pollution may directly affect CSS shrubs, others (Allen et al. 1997, Padgett and Allen 1999) have argued that the seasonal fluctuations in pollution loading may mitigate the potentially harmful effects of some atmospheric pollutants. In areas such as the Riverside basin, atmospheric pollution loads during the active spring growing season are low. The highest pollution loads occur during the summer when the leaves of most drought deciduous, perennial species in CSS have already begun to senesce and, therefore, the effects of atmospheric pollutants on these plants would be minimized. Nitrogen deposition from atmospheric pollution, on the other hand, increases inorganic nitrogen loads in the soil and might affect plants even when atmospheric pollution is not at peak (Allen et al. 1997, Padgett and Allen 1999). In an effort to explain declines in shrub cover in the highly polluted Riverside Basin, researchers have studied nitrogen deposition effects on CSS. These studies focus on the a hypothesis suggesting high nitrogen deposition not only negatively effect on native shrubs directly, but also positively effects the growth and competitive abilities of exotic annual grasses, which then contribute to CSS decline.

Allen et al. (1997) found study areas with high nitrogen (N) deposition had qualitatively reduced native shrub cover and increased exotic annual grass cover compared to low pollution sites. However, experiments showed both exotic grasses and native shrubs had similar growth responses to N fertilization in the field and greenhouse, suggesting N addition does not necessarily harm or favor one functional group over the other. Additional greenhouse experiments showed some native shrubs responded to N fertilization with increased growth well beyond the levels of some common exotic annuals (Padgett and Allen 1999) and Westman (1976) found fertilization with N and phosphorous enhanced the ability of native CSS shrubs to successfully re-invade disturbed sites. Thus, greater N uptake and use by exotics does not appear to be a causal mechanism of increased cover of exotics and decreased cover of native shrubs in high pollution areas. Instead, competition with exotic grasses appears more important to native shrub survival than increased N. Allen et al. (1997) found *Artemisia californica* seedlings planted in plots from which exotic annuals were weeded grew larger and had increased survival compared to seedlings in unweeded plots regardless of N addition.

Despite initial increases in shrub growth following fertilization, some have argued high levels of soil N may, nonetheless, contribute to shrub mortality. Zink and Allen (1998) suggested increased nitrogen availability was associated with decreased survival of CSS shrubs on a restoration site, but potentially confounding factors such as water availability and exotic abundance were not apparently controlled. Allen et al. (1997) noted early senescence and mortality of *A. californica* seedlings under high N fertilization conditions in the greenhouse, suggesting a toxic effect of N at very high levels, but it is not clear if such high levels would be maintained under field conditions. Alternately, increased shrub growth in response to N fertilization may represent an inability to restrict growth and prepare for dormancy under high N conditions which may lead to increased mortality of shrubs, as hypothesized by Padgett & Allen (1999).

High levels of nitrogen deposition could also indirectly influence shrub survival through effects on organisms, such as mycorrhizal fungi, which engage in symbiotic relations with some CSS shrubs. Mycorrhizal fungi generally benefit host plants by increasing availability of water and a variety of nutrients. Egerton-Warburton and Allen (2000) evaluated changes in diversity and abundance of arbuscular mycorrhizae (AM) in CSS along a N deposition gradient. Increases in N were associated with the displacement of larger-spored species of *Scutellospora* and *Gigaspora*, proliferation of small-spored *Glomus* species, and reductions in AM species richness and diversity. The authors argued the proliferation of *Glomus* spp. in high nitrogen deposition sites may contribute to declines in the CSS shrub community over time as these AM species exhibit a more parasitic relationship with host species than the AM species displaced by nitrogen enrichment.

The overall effects of atmospheric pollution on the CSS community are not entirely clear. Though replacement of CSS by exotic annuals has been associated with high pollution levels, other influential disturbance factors have not been adequately controlled. However, some evidence suggests high levels of atmospheric pollution may be related to declines in CSS shrubs either directly or indirectly. Which shrub species might be most sensitive, if any differences exist, is unknown. Thus, it is difficult to predict if and how CSS community composition might change in response to high pollution levels. It is also difficult to predict how quickly shrubs will respond to pollution since the mechanisms through which they might be affected are not certain. Though not as well-studied, native herbaceous perennials may also be negatively affected by atmospheric pollution since the growing season for these species extends further into the summer when pollution loads are nearing the maximum

(O'Leary and Westman 1988). Increased pollution has also been associated with increased abundance of exotic annuals, although it is not clear high levels of atmospheric pollutants directly facilitate the spread of exotics. Declines in native perennials in CSS might result from direct or indirect effects of high pollution levels creating openings suitable for the spread of exotics already present in the system.

Habitat Fragmentation

Habitat fragmentation is often associated with losses in native species diversity, particularly losses of rare species, coupled with increases in exotic species. The factors contributing to species loss are complex and involve reductions in space and resource availability, changes in population dynamics, and changes in a variety of potentially important habitat features that may render the environment unsuitable for some species (Saunders et al. 1991). Species loss may occur both rapidly during the initial period of fragmentation and more slowly over time, depending on longevity and other characteristics of the species involved, making the full impacts of fragmentation difficult to asses (Saunders et al. 1991). CSS vegetation contains many rare species, which might be vulnerable to the effects of fragmentation (O'Leary 1990a). Although fragmentation and isolation of CSS have been occurring at a rapid pace, few studies document the effects of fragmentation on the CSS vegetation community. Studies of fragmentation effects in similar Mediterranean vegetation types might provide some insight into the potential long-term effects of habitat fragmentation on the CSS vegetation community.

Alberts et al. (1993)conducted surveys for native and exotic plant species (excluding grasses) in CSS canyon fragments in San Diego County, CA to determine the effects of fragmentation on CSS vegetation composition and the factors influencing compositional changes. Results showed fragment size, perimeter, and age, along with presence of supplemental water, were important predictors of native and exotic species richness. Specifically, larger and more recently isolated canyon fragments, independently, had greater native species richness. Exotic species richness, on the other hand, increased as canyon fragments aged. Large numbers of exotic and ruderal weeds were associated with long fragment perimeters, or increased edge, while supplemental water was associated with higher numbers of escaped ornamental species. Although native species richness declined and exotic species richness increased with fragment age suggesting natives were replaced by exotics over time, neither exotic species richness nor presence of exotic species known to strongly compete for resources were strong predictors of native species richness. According to the authors, this result suggests competitive interactions between exotic species and natives are less important than habitat alterations in explaining the shifts in species composition over time. While habitat alterations likely contribute to losses of some species, the exclusion of exotic annual grasses as a potential predictor of native species richness in this study may be important. Since these exotics are strong competitors (e.g. Eliason and Allen 1997) and are often relatively abundant invaders, including them in the analyses may have shed light on competitive interactions. Exotic annual grasses can increase in habitat fragments and may be at least partially responsible for some native species loss over time. For example, a study of fragmented coastal sage-succulent scrub in Baja California (Escofet and Espejel 1999) found the exotic grass *Bromus madritensis ssp. rubens* accounted for most of the annual cover in habitat fragments of all ages. *Bromus* was absent from the unfragmented control area, supporting the association between fragmentation and invasion by exotic grass. While not directly discussed by the authors, their data also suggested species loss occurred in fragments over time since older habitat fragments contained only ~52% of the species found in the unfragmented control while newly fragmented patches contained ~83% of those species.

The studies above imply that fragmentation of CSS is associated with localized native species extinctions over time. Due to the lack of pre-fragmentation data, it is impossible to determine which plant species are most vulnerable to extinction pressures. Rare species, which often have small population sizes or are patchily distributed, or both, are generally believed to have high extinction vulnerability due to initial exclusion or subsequent, isolation-related reductions in genetic diversity. A study in renosterveld vegetation by Kemper et al. (1999) suggests rare species may not always be vulnerable, however. Renosterveld is a mediterranean-type shrubland in coastal South Africa that has similar physiognomic features to CSS and many rare plant species. Kemper et al. (1999) found no relationship between occurrence of locally rare species in fragments and fragment size. Although the effects of fragment isolation or dispersal abilities of rare species were not specifically investigated, the authors suggested the naturally small and isolated populations of rare species "may well have been resistant to inbreeding depression and loss of heterozygosity" (p. 109), thus, buffering the populations against adverse genetic effects associated with fragmentation. However, the authors also acknowledged the overall weak effects of fragmentation found in their study might have been due to relatively recent fragmentation, implying these species could disappear over time. Plant attributes related to fragment size were best explained by changes in disturbance regimes within renosterveld fragments. In particular, smaller fragments, which have a higher proportion of disturbed edge, had greater numbers of exotic, annual species, including annual grasses. This, again, demonstrates fragmentation is associated with exotic plant invasions, though such invasions are probably related to disturbances other than fragmentation itself.

The biological effects of habitat fragmentation are varied and complex. It can be difficult to predict which species are most vulnerable to fragmentation, as this will largely depend on the habitat type and attributes of individual species. In addition, as fragment size decreases, the effects of other disturbances may increase and compound problems associated with fragmentation alone. In CSS vegetation, habitat fragmentation is of increasing concern, and fragmentation has been associated with reductions in native species and increased exotic species invasion. While it may be difficult to predict changes in native species composition as a result of CSS fragmentation, exotic species invasions could play a role in some native species losses and decreases in habitat quality.

Disturbance and Exotic Plant Invasions

The process of exotic species invasion is complex, and much remains unknown about the factors contributing to successful invasions. Most immigrant species never become successfully established in new environments, and of those doing so many become naturalized and are not problematic invaders (Groves 1986, Mack et al. 2000). However, the small percentage of immigrants which do become invasive can cause extensive damage to natural systems (D'Antonio and Vitousek 1992, Schierenbeck 1995, Mack et al. 2000). While some generalities exist with respect to invasions and invaders, it is difficult to predict whether or not an alien species will become invasive. Many invasive plants share common characteristics such as rapid growth, continual and/or prolific reproduction, high dispersal ability, and the ability to survive a variety of environmental conditions (Lepart and Debussche 1991, Schierenbeck 1995). However, it is not always obvious how such traits promote invasion within a specific habitat. It is also unclear whether some plant communities are more or less invasible than others, though vegetation structure may be important (Mack et al. 2000). Among vegetation communities in southern California, CSS may be more susceptible to invasion than chaparral due to its open canopy, but less altered by invasion than grassland or oak woodland (Rundel 2000). Within CSS as a whole, some stands may be more or less susceptible to invasion than others. For example, the dominance of certain plants, such as Salvia mellifera, has been associated with low herbaceous cover (Giessow 1997). Thus, invasion by exotic herbs might be inhibited in such stands if the shrubs have a strong moderating influence on both native and exotic herb growth. Certain environmental variables may similarly affect invasibility of a CSS stand. Herb cover is often lower on south facing slopes in CSS (O'Leary 1990b, Minnich and Dezzani 1998), so rates of invasion by exotic herbs might also be expected to be lower due to the environmental factors which limit native herb growth. Alternatively, because the understory is open, invasion might be higher on southern exposures if the environmental factors do not negatively affect particular invaders. Giessow (1997) found that exotic plant biomass in CSS stands was not correlated with slope or soil variables. This illustrates the difficulties in predicting where exotic species invasions will most readily occur. Yet, disturbance frequently plays a role in the invasion process.

Disturbance within a vegetation community is frequently associated with exotic plant invasions, as described above for CSS. In general, disturbance likely facilitates the invasion process by creating openings in the community which invading species then occupy. Whether some level of disturbance is necessary for some invasions to successfully occur is not always clear. Burke and Grime (1996) found the susceptibility of a grassland community to invasion was strongly related to disturbance intensity. In California, Rundel (2000) showed exotic species made up a relatively large portion of the flora of the Santa Monica Mountains, yet they were largely restricted to heavily disturbed areas and had not become significant components of plant communities outside these areas. Minnich and Dezzani (1998), on the other hand, suggest some exotic species, including some common exotic annuals in California, may have the ability to invade undisturbed habitats and competitively exclude native species. Potential evidence for invasion of undisturbed, mediterranean shrubland is provided by Lambrinos (2000), who described an invasion of presumably undisturbed chaparral by *Cortaderia jubata* (jubata grass, pampas grass), an exotic perennial grass. In his study, however, the initial establishment of *C. jubata* in the area followed a large disturbance associated with construction, and subsequent spread into "undisturbed" chaparral was usually associated with small-scale disturbances such as stream channel erosion. This demonstrates the complex relationship between disturbance and exotic invasion. Part of this complexity comes from the great variety of disturbance types and intensities that might influence invasion. Once an invader is present in a system, even small and natural disturbances can create suitable micro-sites for population expansion and may ultimately facilitate the spread of the invader. It is likely the level of disturbance required, if any, for initial establishment and subsequent spread varies by invading species and by habitat (see Lepart and Debussche 1991 for additional discussion). Invaders who outcompete native species or have better dispersal abilities may require lower levels of disturbance and may spread more rapidly through a community.

Regardless of the disturbance level preceding an invasion, the invasion process itself often constitutes a disturbance. Exotic plant invasions change community composition both through the establishment of the invading species and competitive exclusion of native species. These compositional changes may produce changes in vegetation structure and the quality of habitat for other taxa. Food-web structure is likely affected as native plant species are excluded by the invader or if the invader attracts additional competitors or predators (Mack et al. 2000). Exotic species invasions can also disrupt community dynamics such as nutrient cycling, energy budgets, and natural disturbance regimes that, in conjunction with competitive forces, may interfere with the maintenance or post-disturbance regeneration of the original vegetation community (D'Antonio and Vitousek 1992). As discussed previously, for example, high cover of exotic grasses in mediterranean-type shrub communities in California has been associated with unusually short fire return time and subsequent vegetation-type conversion (Zedler et al. 1983).

Because exotic species invasions often co-occur with other disturbances directly affecting plant community composition and structure, it is difficult to ascertain the independent effects of invasions on vegetation communities. However, in relatively undisturbed chaparral, invasion by *C. jubata* was associated with declines in native plant species richness, changes in vegetation structure, and declines in arthropod and small mammal diversity and abundance primarily due to the reduction of native shrubs and subshrubs (Lambrinos 2000). While the reduction of chaparral shrubs in this study cannot be directly attributed to invasion with absolute certainty, the higher cover of dead shrubs in invaded areas suggests *C. jubata* may be an effective competitor for critical resources. Other studies provide evidence for the competitive abilities of some exotic annual grasses and the potential for exclusion of native CSS shrubs by these exotics. For example, Eliason and Allen (1997) showed germination and first season growth of *Artemisia californica* were negatively related to exotic annual grass density near seedlings. Depletion of soil moisture by the early germinating and fast growing grasses was proposed as the most likely cause of *A. californica* seedling mortality. Padgett and Allen (1999) also found decreased survival of native CSS shrub seedlings competing with exotic grasses (discussed above). These studies suggest exotics, through competition, may interfere with shrub recruitment in invaded CSS, and could result in vegetation-type conversion over time. Replacement of naturally occurring CSS stands by exotic species has been noted in the Riverside-Perris Plain where large declines in native shrub cover since 1932 correspond with increases in cover of exotic annual grasses (Minnich and Dezzani 1998). Other than fire occurrence, complete disturbance histories were not discussed for these study sites, but may also have impacted native plant associations.

The vulnerability of the CSS vegetation community to replacement by exotic species in the absence of repeated or intense disturbance is not clear. Despite the evidence of competition between exotic annual grasses and native CSS shrub seedlings, CSS shrub succession is known to occur within areas dominated by exotic species once disturbance has been eliminated or reduced. For example, shrub succession has been noted in exotic annual grasslands where grazing has been discontinued or decreased (McBride 1974, Oberbauer 1978, Freudenberger et al. 1987). In their study of mechanical disturbance on CSS shrubs, Narog et al. (2000) found that shrub seedling recruitment was successful in the disturbed area despite initial site domination by exotic annuals. Similarly, Westman (1976) found native CSS shrub species were able to recruit seedlings and successfully re-establish in an area planted with several exotic species after deliberate shrub removal. As discussed above, however, in both of the latter studies supplemental water was provided in most cases and, as specifically noted by Westman (1976), likely enhanced shrub regeneration on the disturbed sites. Eliason and Allen (1997) found the negative effects of exotic grass density on shrub seedling survival did not persist beyond the seedling's first growing season. Thus, in heavily invaded areas where shrub seedlings must compete with exotics, additional moisture availability during the first active growing season for shrub seedlings might substantially influence the rate of CSS post-disturbance recovery or stand maintenance. The availability of suitable gaps for seedling recruitment and the dispersal abilities of both natives and exotics in the community are probably equally or more important. Although a few CSS shrubs appear to be effective dispersers capable of competing with exotics for gaps, it appears that other native species might not compete as well.

While some CSS shrub species may be resistant to direct replacement by exotic plants in the absence of repeated disturbance, this potential resistance may not be shared by all shrubs or the herbaceous component and other taxa within the community. Studies have found that cover (Zink et al. 1995) and richness (Davis 1994) of native herbs were lower on disturbed plots where exotic abundance, and sometimes native shrub cover, was high. In the study by Lambrinos (2000), five native herb species found in uninvaded chaparral were not found in near-by chaparral plots invaded by C. jubata. Similarly, Westman (1976) found that 23 species present in mature stands of CSS, at least some of which were undoubtedly native herbs, were absent from plots in which exotics had been planted, even though CSS shrubs had successfully re-established. While absence of a species in these studies is not direct evidence for exclusion by exotic invasion, it does imply that the herbaceous component of CSS vegetation may be vulnerable to replacement by exotics.

Even if some native shrubs are able to tolerate or recover from exotic plant invasions, declines in native herbs or changes in shrub species composition may lead to declines in arthropods or other taxa which utilize those plants, thus affecting food webs. For example, Lambrinos (2000) attributed reduced frequency of hymenoptera in *C. jubata*-invaded chaparral, in part, to the absence of some large-flowered, nectar-rich forbs in invaded stands. In CSS vegetation, increases in exotic annual grasses and forbs may cause declines in the native forb *Plantago erecta* (Stephenson and Calcarone 1999, p. 174), the primary larval host plant of the federally endangered Quino checkerspot butterfly. Finally, a study by Bolger et al. (2001) suggests that some birds may also be sensitive to plant species composition in CSS. A comparison of remnant patches and narrow strips of CSS habit with highway rights-of-way (ROW) revegetated with native shrubs revealed that richness of fragmentation-sensitive bird species was lower in ROW sites than in both types of remnant habitat. Richness of these bird species was positively correlated with shrub cover, but shrub cover did not differ significantly among the 3 habitat types indicating that factors other than vegetation structure were also important for these birds. The authors suggested that shrub composition may be important, but many native herbs were probably also absent from ROW sites, and exotic cover was probably high. In addition to changes in food web and other system dynamics, exotic invasions may also result in changes to the soil microorganism community which could, in turn, affect shrub survival over the long term (Egerton-Warburton and Allen 2000).

The potential for permanent vegetation-type conversion of CSS following exotic species invasion likely depends on a variety of factors including properties of the invading species and the frequency, type, and extent of disturbance. Frequent or intense and widespread disturbances that reduce resprouting capabilities of native perennials and the availability of native seed sources for site recolonization should increase the probability of CSS replacement by easily dispersed, fast-growing, disturbance tolerant exotic species such as the common, exotic annual grasses of Mediterranean origin. O'Leary (1990a) reported a fire return time of less than 5-10 years as potentially resulting in replacement of CSS by exotics, and our literature review indicates this interval may apply to some other disturbances as well. Regardless of the disturbance type, however, the disturbance interval actually resulting in community replacement may vary depending on the invading species. Some long-lived, perennial, exotic species may be more effective competitors with native species and, thus, more capable of replacing them without frequent or large scale disturbances (Westman 1976, Zedler 1988, Lambrinos 2000). Even if vegetation-type conversion does not result, however, permanent disruption of CSS community dynamics may occur with some invasions leading to decreased habitat quality. More research is needed, though, to determine the extent and duration of such disruptions.

Conclusions

The CSS vegetation community appears highly resilient to infrequent disturbance since the dominant shrubs and many herbs quickly regenerate from resprouting individuals or seeds. Frequent disturbance, on the other hand, including combinations of different types of disturbances, may lessen the resilience of many species and make the plant community more vulnerable to replacement by other vegetation, particularly exotic plant species. While evidence suggests some CSS shrub species can re-establish on even highly disturbed sites, it is not clear to what extent other components of the system, including both flora and fauna, share this resilience. Recovery by highly resilient shrub species could mask signs of disturbance in non-dominant components of the system and in ecosystem processes associated with these components. In other words, recovery of CSS shrubs from disturbance does not guarantee recovery of the entire CSS community. In addition, certain types of disturbance, such as fragmentation and air pollution, may affect the dominant shrubs only over long time periods. Other community components may be more sensitive to and respond more quickly to those disturbances. For example, understory herbs in CSS may be replaced relatively quickly by the exotic species invasions associated with these disturbances. However, this may, again, be masked by resilience of the dominant shrubs, so the disturbance effects are not readily visible until the whole community is on the verge of replacement. Thus, attempts to determine levels of disturbance or community disruption in CSS habitat based on native shrub cover may be misleading. Developing a more reliable means of determining the extent of disturbance in CSS would allow better management for community health and long term viability, particularly in cases where land-use records may be insufficient in determining levels disturbance.

There are few clear trends in the response of CSS vegetation to different types of anthropogenic disturbance. This may be due, in part, to the heterogeneous nature of the CSS vegetation community as a whole. Native species composition and cover is highly variable at several scales and may be related to both environmental variables and disturbance history. Regardless of the type of disturbance, however, increases in the abundance of exotic plant species occur as disturbance in CSS becomes more frequent or severe. In addition, the increases in exotic species that typically accompany disturbances in CSS may remain as evidence of disturbance even if shrubs recover. Once a successful invasion has occurred, exotics appear to persist in the community for some time. For example, Davis (1994) found no evidence exotic species abundance was decreasing on disturbed sites even more than 70 years after disturbance. The persistence of exotic plants may represent the long-term effects of past disturbances, and may be indicative of community disruption.

Since increased abundance of exotic plant species appears as the most common response to a variety of disturbances in CSS, and since the invasion process itself constitutes a disturbance, it seems reasonable to utilize exotic plant species abundance as a coarse measure of disturbance within CSS habitat. While such a measure will not be able to distinguish among different types or mechanisms of disturbance, it should provide a rough indication of the extent of disturbance, with greater exotic abundance indicating greater habitat disturbance. However, it remains to be determined what this measure of disturbance indicates with respect to community processes and overall health. This can only be accomplished by examining several elements of the system under different levels of invasion. Such research will be valuable to the development of a reliable indicator of current community condition and habitat quality and may provide insight into future trajectories of the vegetation. A reliable indication of community condition will aid in the development of management strategies designed to enable recovery of disturbed CSS, where possible, and to ensure long-term viability of the entire CSS community.

Data Gaps and Recommendations for Further Research

Several questions remain with respect to disturbance and exotic plant invasion in CSS. Although the studies discussed above suggest a strong positive relationship between disturbance and invasion, designing future studies to examine the relationship more closely should produce fruitful results. Potential questions include:

- Are some exotics species favored to a greater degree than others by any disturbance, or specific types of disturbances in CSS?

- Are some native species or functional groups in CSS more or less sensitive to replacement by exotics, and does this sensitivity change with different levels and types of disturbance?
- How, specifically, does exotic invasion and replacement of native species, if it occurs, affect whole-community dynamics?
- Is any community disruption associated with exotic invasion permanent, or can CSS stands recover over time?

Because many exotic annual species are seemingly ubiquitous throughout California's natural vegetation communities, the possibility of these species reaching equilibrium within the native community is real. If such equilibrium exists, it can only be determined by concomitant examination of multiple components of the community. An abundance of exotic species, including both the common annuals and other, more aggressive exotics, may be associated with disruption of critical, but less readily visible, community processes including food web dynamics, and nutrient cycling. Whether the processes are permanently disrupted or the community will recover over time likely depends on factors such as the presence of particularly aggressive, exotic species and future levels of disturbance. We expect a threshold of tolerance to invasion exists within the CSS plant community. Below this threshold, habitat quality may vary, but the community can recover and quality can improve over time if properly managed. Once this threshold is surpassed, however, the disrupted community processes may make recovery impossible, and vegetation-type conversion is, perhaps, inevitable.

If such a threshold exists and can be quantified, it will provide useful information to land managers. In order to realize the full benefits of this kind of information, however, we must learn more about the dynamics of disturbance and invasion so appropriate management decisions can be made to prevent further degradation of disturbed, but recoverable, habitat. Answering these questions will require much research. Designing studies to help answer these questions might also help us answer more general ecological questions regarding disturbance effects, exotic species invasions, and ecosystem function that can be applied both within CSS and other vegetation communities.

Mammals

Introduction

There are many reasons small mammals might be useful indicators of disturbance in CSS systems. Because of their abundant numbers, high reproductive rates, and broad diets, small mammals play a vital role in nearly every ecosystem in which they have been studied. For example, small mammal herbivory and granivory can influence rates of production, alter species composition (Mills 1983, DeSimone and Zedler 1999), and change patterns of post-disturbance succession in vegetation communities (Mills 1986, Ostfeld and Canham 1993), Davidson 1993. Work by J. Brown and his students show small mammal seed predation maintains desert scrub communities in the arid southwest. In the absence of this predation, the areas would convert to arid grasslands (Brown and Heske 1990). Other studies indicate small mammal herbivory and predation limits population sizes of terrestrial arthropods (Batzli & Pitelka 1970). Additionally, small mammals are key prey items for snakes, raptors, and medium-sized mammals such as coyotes and bobcats and may play a role in limiting the population sizes of such predators (Bowyer et al. 1983). As both predators and prey items, small mammals interact with numerous trophic levels within a food web and thus play a critical role in determining species diversity and composition within an ecosystem.

In addition to crucial roles in many food webs, numerous studies demonstrate small mammals often respond directly to disturbances. Small mammals are well known for responding directly to both physical structure and species composition in plant communities. Indeed, many studies suggest small mammals may show large responses to fire, invasive species, habitat fragmentation and isolation, and edge effects.

Fire

Fire is recognized as a primary factor affecting both the distribution and species composition of CSS flora and fauna. The density of plant cover, in combination with southern California's arid Mediterranean climate, makes CSS one of the most fire-prone vegetation types in the world (Hanes 1971). Despite many studies on the responses of CSS vegetation to fire and its consequent succession, little research has been done on the responses of CSS mammals to fire and post-fire faunal succession.

Fire can directly kill individuals through incineration and asphyxiation. Fire mortality is most common among small, relatively immobile mammals that lack access to refuge during fire, but even fast moving large mammals, such as deer, can be killed in intense, fast moving fires (Quinn 1994). Sources of refuge during fire can include below ground burrows, rock crevices, rock outcroppings, and spaces beneath logs or stones, where temperatures remain below 138° F (Howard, et al. 1959).

Post-fire impacts on small mammal communities are well studied in a Mediterranean region of Australia similar to southern California. By sampling areas with different ages since fire (substituting space for time), and by sampling a small number of locations for over 20 years, (Fox 1990, 1996) Fox (1982, 1993, 1996) has shown a predictable post-fire pattern of succession in the small mammal community. In the Australian heathlands, small mammal succession occurs because species-specific habitat requirements and interspecific competition varies with temporal changes in vegetation composition (Fox 1996). Fox (1981) also showed succession in heathland small mammals occurs as a replacement of dominant species rather than as a replacement of guilds as sometimes seen in other taxa. Although small mammal responses to fire are not nearly as well studied in southern California's CSS, we feel post-fire succession patterns are likely similar. We describe our reasoning below.

In CSS, fire causes a reduction in cover and food resources and may cause a shift from species preferring dense shrubs and high amounts canopy cover to those that live in more open habitats (Lawrence 1966). Generally, early post-fire shrub sites, such as CSS, are colonized by grassland species such as *Microtus californicus* (California vole), *Reithrodontomys megalotis* (harvest mouse), *Peromyscus maniculatus* (deer mouse), and sometimes the non-native *Mus musculus* (house mouse), rather than species more often found in mature CSS such as *Peromyscus eremicus* (cactus mouse) and *Neotoma lepida* (desert wood rat) (Cook 1959). Typically, as shrub density and food availability increase in the months after a fire, CSS species re-invade the site (Lawrence 1966, Schwilk and Keeley 1998).

In a study of post-fire responses of five small mammal species in CSS, Price and Waser (1984) were able to successfully predict the post-fire relative abundances of co-existing species by understanding their microhabitat use (open, brush, debris, and rock microhabitats). They found *Dipodomys agilis* (pacific kangaroo rat) was the only species that specialized on open microhabitat. *Peromyscus maniculatus* showed a slight preference for debris and *Chaetodipus fallax* (San Diego pocket mouse) preferred rock. *Peromyscus eremicus* and *N. lepida* used both rock and bush microhabitats with approximately equal frequency.

In the burned CSS, fire significantly increased open microhabitat and significantly decreased bush microhabitat. Immediately after the fire, debris was much less abundant in the burned area than in the unburned area. Fire had no impact on the rock microhabitat available. Given these changes in microhabitat, *D. agilis* became consistently more abundant in burned than unburned sites, while the other species were generally more abundant in unburned sites. Thus in CSS, like in the Australian heathlands, a predictable post-fire rodent succession may occur because of species-specific habitat requirements associated with changes in vegetation through time.

It is likely, however, that there is a delay between the time when plant succession creates suitable habitat for an absent species and the establishment of a viable population of that species. The length of the delay will depend on the dispersal rate and the distance to the nearest source of immigrants (Quinn 1994). This implies the recovery rate of the mammal community will depend on both the characteristics of a species, the characteristics of the matrix surrounding a burn, and the size of the burn (Schwilk & Keeley 1998).

Invasive species

Additionally, changes in fire frequency and intensity, often associated with human disturbance, may alter post-fire plant succession and even promote non-native invasion. Frequent burning, for example, has been associated with increased transition rates from CSS to grasslands and the invasion of CSS by exotic annual forbs and grasses (Callaway and Davis 1993). Price (1994) found that small mammal responses to shrub removal in CSS differed by species. While the abundance of *Dipodomys stephensi* (Stephen's kangaroo rat), *Perognathus longimembris* (little pocket mouse), *C. fallax*, and *P. maniculatus* increased in response to shrub removal, the abundance of *Dipodomys agilis* (pacific kangaroo rat) and *P. eremicus* decreased. Given the specific diets (Meserve 1976) and habitat requirements (Price and Waser 1984) of small mammals, it is likely that CSS small mammal species will respond uniquely to changes in post-fire plant succession and the establishment of non-native plant associations.

Habitat Fragmentation and Isolation

Habitat fragmentation is a process that degrades a continuous habitat into smaller patches. Though habitat fragmentation can occur through natural processes such as fire or windfall, the most large-scale cause is the expansion of human land use (Andren 1994). Habitat fragmentation has three major impacts; loss of original habitat, reduced habitat patch size, and increased isolation of habitat patches.

Habitat loss generally results in decreases in native species abundance. Reduced patch size and increased patch isolation typically results in decreases in species richness in habitat fragments. This pattern is well established from both empirical studies of habitat fragmentation and a long history of research into the theory of island biogeography (MacArthur and Wilson 1967, Rosenweig 1995)). Decreases in patch size might also result in smaller effective populations and decreased genetic diversity. Additionally, habitat fragmentation may affect interspecific interactions and ecological processes, such as competition and predation, possibly intensifying any original fragmentation effects (Debinski and Holt 1998).

Ecologists have studied small mammal responses to habitat fragmentation both experimentally and in naturally patchy systems more so than many other taxa (Lidicker 1995, Barrett and Peles 1999). Small mammals are relatively easy to study given the small spatial scale at which populations exist, and the ability to mark and recapture individuals. In a review paper, Debinski and Holt (2000) concluded studies have indicated some support for the expected decreases in species abundance and richness with decreased fragment size, but have also demonstrated changes in movement rates, distances, and spatial patterns, as well as changes in home range sizes and overlap.

Though remaining CSS is highly fragmented, the impacts of this patchy landscape on small mammals, as well as many other organisms, have not yet been thoroughly studied. In one study (Bolger et al. 1997a), small mammal distributions were surveyed by live-trapping at 25 fragmented CSS/chaparral sites and 3 relatively unfragmented CSS/chaparral sites in coastal San Diego County. Isolated sites varied in percent shrub cover, size, time since isolation, and distance from a mainland, but were all completely surrounded by human-modified habitat. Rodents were trapped from 2 to 5 times at each site during 1986-87 and then 12 of the 25 sites were surveyed again in 1992 to assess exctintion and recolonization events. The authors found an assocation between high abundances of native small mammal species (*Neotoma fuscipes* (dusky-footed woodrat), *Peromyscus californicus* (California mouse), *P. eremicus*, *C. fallax*, *N. lepida*, and *R. megalotis*) and more recent time since isolation; higher percentages of shrub cover; and shorter distances from unfragmented sites; and the absence of *Rattus rattus* (Black rat).

Small mammals were not found on 13 of the 25 fragment sites. These 13 sites were generally smaller than fragments that did support populations of native small mammals. The size of a fragment site was the primary determinant of species diversity. In addition, fragments supported fewer species than equivalently sized plots in unfragmented habitat and older fragments (isolated for longer periods of time) supported fewer species than younger fragments. The isolation distance of a fragment had no relationship to species diversity. These results indicate that relatively rapid local extinctions occur within the small, urban fragments and are predictable based on species abundances in non-fragmented areas (i.e. species that are typically abundant everywhere are less likely to go extinct when isolated in a fragment). Also, the area of shrub vegetation at a site was a better predictor of the number of native small mammals at that site than the fragment's total area. This indicates that small mammals native to CSS may not often use non-native herbaceous vegetation and emphasizes, once again, the importance of microhabitat availability. Lastly, high numbers of native small mammal species were associated with the absence of the non-native *Rattus rattus* (Black rat) at a site, indicating competition between native and non-native small mammals for resources in CSS systems.

Edge Effects

Because habitat fragmentation inevitably creates a matrix of qualitatively different habitats, edge area is increased. Increasing the amount of edge can have enormous impacts on a system. Increased edge can subject a system to changes in abiotic conditions such as wind and temperature. Changes in abiotic conditions can result in altered vegetation communities and processes such as nutrient cycling. Increased edge can also make a system vulnerable to biotic changes such as invasion by non-native species. Changes in biotic and abiotic conditions resulting from increased edge can profoundly alter ecological processes such as competition and predation (Debinski & Holt 2000).

In general, small mammals seem to respond strongly to habitat alteration and exhibit species-specific responses depending on their habitat requirements (Sauvajot et al. 1998). Because small mammals respond directly to both physical structure and species composition in plant communities, as well as to disturbances within those communities, species abundance often varies both with distance to an edge and with type of edge (Weber 1995, Sauvajot et al. 1998). Potential effects of edges include changes in resource availability (food or habitat) and competition, changes in predation or other types of direct mortality such as road mortality, (Adams and Geis 1983), and avoidance behavior (i.e. avoidance of anthropomorphic lights, sounds, or smells).

CSS is, to a large extent, surrounded by an urban matrix. Evidence suggests that native small mammals may respond strongly to urban edges. Non-native species often associated with urban development, such as the Argentine ant, may compete with small mammals for food resources and infest nesting areas (Suarez 1998). Some studies also suggest that native species may compete with non-native species such as *R. rattus* and *M. musculus* near urban edges and possibly be displaced by them (King 1957, Bolger et al. 1997b).

Probably the strongest edge effect confronted by CSS small mammals is predation by domestic cats. Crooks & Soule (1999) found evidence for “mesopredator release” throughout the fragmented CSS canyons of southern California. Decreases in large mammalian carnivores such as coyotes and mountain lions in CSS fragments allow for increases in medium-sized predators (mesopredators) such as domestic cats. Domestic cats are recreational hunters subsidized by humans and are extremely effective predators of small mammals. It is likely that the presence of domestic cats greatly decreases small mammal abundances near urban edges.

Conclusion

The above review suggests mammals, and small mammals in particular, may show measurable responses to certain forms of disturbance and may be effective in an IBI for CSS. CSS mammals will exhibit responses primarily to changes in the vegetation community, and perhaps also to alterations in levels of predation and levels of competition caused by disturbance. While many forms of disturbance will impact mammals directly, perhaps most of the impacts will result from complex, difficult to understand, indirect effects. For examples, urban edges may directly impact small mammal communities because some species are intolerant to the increased light and noise levels. However, with urban edges come domestic cats, non-native small mammals, altered hydrology, argentine ants, invasive plants, and perhaps altered fire regimes. The literature review leads us to cautiously conclude disturbance to CSS will likely have larger indirect effects on small mammals, mediated by changes to CSS vegetation, than direct effects. As discussed in the vegetation section above, a fundamental effect of nearly any form of disturbance in CSS is an alteration in the vegetation community.

Given the high levels of habitat selection CSS small mammals perform and the degree of microhabitat preferences exhibited by some species, well-designed monitoring programs should be able to measure responses of small mammals to changes in vegetation caused by disturbance. These responses will likely manifest themselves as changes in the numbers and types of species present in a system. Studies in other systems indicate processes such as fire, predation and competition can create predictable assemblages of small mammals (Fox 1987, Kotler and Brown 1988). Furthermore these assemblages can be predicted by the presence or absence of factors related to these processes (i.e. rainfall, soil type, or particular competing or predatory species).

Fortunately, the few studies of CSS small mammal communities were well-designed and implemented (Meserve 1972, 1976, Price and Waser 1984). These documented the diets, foraging behaviors and microhabitat use of CSS small mammals and suggest the presence of particular species can be associated with specific processes. Because the diets, foraging behaviors, and microhabitat use of CSS small mammals are somewhat species-specific, it is likely that some members of the community will respond uniquely to disturbances within the CSS system. For example, we hypothesize *N. lepida* and *P. eremicus* presence in older, closed stands of CSS, and absence in disturbed CSS dominated by grasses. Furthermore, we except *M. Californicus* presence in moderately to highly disturbed sites with high amounts of grasses. Finally, we expect the presence of non-native *M. musculus* and *R. Rattus* only at disturbed cites near urban edges.

Predation and competition, particularly at edges, may influence the species composition of CSS small mammal communities. However we currently lack a good understanding of how, and to what extent, these two processes actually determine the presence or absence of species in specific areas. Dr. Douglas Kelt, at UC Davis, recently completed a three-year study of CSS small mammal communities. When analyzed, these data should indicate the relative strength of competition between CSS small mammal species and it's role in structuring the community.

Placing Small Mammal monitoring data in an IBI.

Unlike other taxa that contain many species, we expect monitoring programs in CSS to never catch more than 16 species. This small number of species makes placing them in a typical IBI guild framework with functional, compositional and structural components somewhat difficult because false absences (not detecting a species, when it is truly there) will have a large impact on a guild with only 3 species and potential cause large amounts of error around an IBI score for small mammals. We have created a working guild framework for small mammals (Table 2). However, we will likely develop an alternative scoring mechanism for small mammals or combine some guilds. Our field studies will allow us to determine the effectiveness of the standard IBI scoring protocols and make necessary modifications.

Table 2, Potential Small Mammal Guild Attributes and species categories for Measuring CSS Habitat Disturbance*

Integrity Element	**Guild Category**	**Response Guild (%)**	**Specialist**	**Generalist**	**Species**	**Metric Rating**		
						5	**3**	**1**
Functional	trophic	Omnivore		x	P. californicus, P. maniculatus, P. erimicus,			
		Carnivore	x		Onychomys			
		Granivore	x		R. megalotis, P. longimembris, C. fallux, D. agilis			
		Herbivore	x		N. lepida, N. fulvesense			
Compositional	origin	exotic		x	M. musculus, R. rattus			
		resident	x		ALL			
Structural	Primary habitat	Closed canopy, high levels of 3- D structure	x		N. lepida, N. fulvensence, P. ermicus			
		Open CSS	x		D. agilis,			
		Grasslands, disturbed CSS		x				

*Adapted from O'Connell, et al, 2000, Croonquist & Brooks, 1991, and Karr, 1991. Scoring to be determined.

Data Gaps and Recommendations for further research

Though thorough, high quality scientific research on mammals in CSS exists, the total number of studies is small and hence our current understanding of the processes structuring mammalian communities in CSS and their response to disturbance is underdeveloped. Given the strong evidence showing small mammal microhabitat preferences, differences in diets, and habitat selection, we expect small mammal species composition to track changes in vegetation, as it does in similar systems around the world. Thus, understanding how, over time scales of 10-30 years, small mammal communities track (or do not) changes in CSS vegetation as it is disturbed and recovers (i.e. succession after fire), or is invaded by non-native species, will play a key role in our ability to understand and predict responses to disturbance. Furthermore, we must also understand how both individual species and entire communities of small mammals respond to the little studied processes such as predation and interspecific competition and how the strength of these processes varies with disturbance, in particular distance from edges. Once we better understand the interactions affecting the presence and absence of species in CSS, we will be able refine the use of small mammal monitoring data in IBI's and better understand processes affecting small mammal communities through time or across space and make more informed management decisions.

Birds

In terrestrial systems, birds have been utilized more than other taxa when relating biological metrics to habitat quality and ecological condition (Croonquist and Brooks 1991, Lynam 1996, Bradford et al. 1998, Chase 1998, Fleury 1998, Chase et al. 2000, O'Connell et al. 2000). Birds are considered good indicators of habitat quality for a number of reasons (Lovio 2000, O'Connell et al. 2000). First, many studies show rapid and large responses in bird communities to habitat fragmentation. Second, community structure is often strongly tied to habitat type. Third, birds are known to feed at different trophic levels (arthropods and other invertebrates versus fruits, nectar, and seeds) depending upon seasons and conditions.

The presence or abundance of single species, rare species, and guilds of various combinations have all been used to relate data collected on birds to habitat quality. In many cases, researchers studied the effect of habitat condition, such as fragmentation, on birds (Bolger et al. 1991, Soule et al. 1992, Lovio 2000). Other studies considered the use of particular species as indicators of total species richness and/or abundance within a habitat (Boulinier et al. 1998, Chase 1998, Nichols et al. 1998, 2000). However, only a handful of studies have attempted to connect the richness or abundance of birds with the health of a habitat. Several very encouraging studies illustrate the promise of using birds as one of the primary indicators of habitat health and are discussed below (Croonquist and Brooks 1991, Bradford et al. 1998, Canterbury et al. 2000, O'Connell et al. 2000).

Avian Response to Habitat Fragmentation and Urbanization

Given the relative ease of sampling species presence and absence, avian response to large-scale habitat fragmentation is relatively well studied when compared to other taxa. Studies done across disparate habitat types, countries, and levels of fragmentation nearly all show a decline in native birds as landscapes become more fragmented. In addition, a number of studies have begun untangling the complex causes of bird declines in fragmented landscapes. These vary from a loss of habitat, to increased predation and nest parasitism along patch edges, to changes in species composition and local or regional extinction of species (Renjifo 1999). Interestingly, in many systems studied, a subset of species responds to fragmentation. For example, fragmenting of shrubsteppe habitats by human-caused disturbance or by fire affects obligate bird species, while species not specializing on the shrubsteppe habitat specifically, fare better in fragmented landscapes (Knick and Rotenberry 1995). In another example, loss or conversion of ~94% of the original habitat to agricultural use in the wheatbelt region of S. W. Australia caused a decrease in range and/or abundance in 34 of 109 species of birds and an increase in 9 species (Saunders 1993) Our literature review strongly suggests the native bird community inhabiting CSS likely shows similar, generally negative responses to habitat fragmentation and will be a key element in the development of an IBI.

Landscape patterns of habitat fragmentation and urban/habitat edge are important determinants of birds in coastal southern California. When housing developments, and their associated roads, shopping complexes, and industrial/business sites replace CSS, fragments and edges are created. Two studies suggest an interesting response of CSS avifauna to habitat fragmentation. First, the overall diversity of birds in suburban communities does not change relative to the diversity found in the area prior to development (Guthrie 1974, Vale 1976). However, the *composition* of species is altered as native CSS species are replaced by both non-native exotics and a set of species that persist in urban environments.

This result is caused by species-specific responses to habitat fragmentation. Bolger, et al, 1997, found unique responses of 20 of the most common bird species to fragmentation and edges in the urban landscapes of southern California. Species ranged in response from reductions to increases in abundance with increased levels of edge and/or fragmentation. In approximately half the species, abundance in natural habitats was positively correlated with position in the landscape relative to urban development. Furthermore some species were abundant, widely distributed and showed no sensitivity to landscape position or shrub habitat type. Edge/fragmentation enhanced species such as House Finch, Northern Mockingbird, Lesser Goldfinch, and Anna's Hummingbird, tended to make up the losses of edge/fragmentation sensitive species, such as Black-chinned Sparrow, Sage Sparrow, Lark Sparrow, Rufous-crowned Sparrow, and Costa's Hummingbird, creating the mechanism by which overall diversity does not change yet species composition does -- as found by (Guthrie 1974, Vale 1976).

Ten of the species were considered insensitive to edge or fragmentation effects (Bolger et al. 1997c). Some, like the Rufous-sided Towhee, Wrentit, California Quail and Bewick's Wren, are mainly restricted to the shrub habitats in the region while others, such as the Scrub Jay, Mourning Dove, California Towhee, Common Bushtit and California Gnatcatcher, are know to commonly reside and breed in residential areas, but with lower abundances near edges.

Work by Lovio (2000), also shows species-specific responses to fragmentation of CSS habitat. Lovio studied breeding bird assemblages in 36 CSS fragments ranging from 0.3 - 420 ha. Fragments selected were undisturbed, included less than 5% woody non-native vegetation (by area), and generally separated from other CSS fragments. In some cases areas of disturbed vegetation, including some CSS species, connected sites. Lovio (2000) found the bird assemblages exhibited a low response threshold to fragmentation. Area-sensitive species quickly dropped out of patches, even relatively large patches. A larger proportion of species in the assemblage appeared relatively unaffected by habitat fragmentation, though this study did not focus on detailed demographic responses. Additionally, some generalist species were enhanced on small fragments.

Bolger, et al.'s work (1991) and work done by Crooks and Soulé (1999), further elaborate on potential mechanisms causing declines in bird communities. Bolger et al (1991) showed the rapid extinction of resident birds in fragmented chaparral was a function population density. There was a strong positive correlation between relative persistence ability and population density. Furthermore, population density was influenced by patch size. Thus, processes such as demographic stochasticity, perhaps caused by large fluctuations in reproductive output associated with rainfall, may lead to local extinctions of birds from smaller, isolated patches. We assume similar processes could occur in CSS habitat.

Crooks and Soulé (1999) found fragmented coastal sage scrub and chaparral habitats resulted in the local extinction of top mammalian predators (coyotes) as patch sizes reached minimum thresholds. This loss of top predators was correlated with an increase in avifaunal presence, and negatively correlated with the presence of mesopredators (skunks, domestic cats, possums, etc.). These results suggest mesopredators may regulate populations of birds in CSS patches. Furthermore, in highly fragmented systems, a loss of top predators may release mesopredators from competition and/or predation and greatly increase the predation pressure on birds, leading to their extirpation from patches. (see also Soule et al. 1988).

In summary, fragmentation of, and edge effects in, CSS habitat tends to cause a reduction in obligate avian species and often attracts species adapted to suburban environments and to the boundaries of such environments. The result is often an increase, or at least no decrease, in species richness in CSS habitat, particularly near edges of fragmented patches. However, species composition changes as CSS obligate species drop out of the system and are replaced by urban and edge tolerant species.

Bird Response to CSS Fire

Fire has a substantial effect on CSS vegetation structure and therefore should impact avian communities. Unfortunately, few studies have documented the response of CSS birds to fire. Furthermore, we did not find any studies focusing on the effects of fire history or burn frequency on bird communities. Moriarty et al. (1985) showed an initial drop in species richness and abundance as a result of a fire in CSS on the campus of California State Polytechnic University. The bird community recovered quickly, with 70 – 90% of the original species richness and abundance of birds intact after one year. A study of controlled burning in chaparral by showed a decrease in chaparral birds up to four years after the fire, but an increase in grassland birds as well as a temporary increase in predator birds in both the grassland and chaparral areas (Lawrence 1966). Fire will certainly influence the composition of bird species in CSS immediately after a fire, with recovery to pre-burn status likely following vegetation successional trajectories and timescales. Given the lack of studies, we currently cannot be sure how the avian community responds to the conversion of CSS to grasslands caused by frequent fires. However, given the large differences in species composition between grassland and CSS bird communities, and the apparent obligate nature of some CSS birds, we expect frequent fires to drastically alter CSS bird communities to those associated with grasslands.

Birds as Single Species Indicators

A number of authors have investigated the use of single bird species as indicators of overall species richness, or ecosystem function at a location (Williams et al. 1996, Boulinier et al. 1998, Chase et al. 2000). Because birds are relatively well studied, we chose to review the utility of a single species approach to estimating habitat quality, or indicating some aspect of overall ecosystem health. Our review has convinced us single species approaches work poorly, especially when compared to the guild or community-based approaches we describe below. A number of studies have come to similar conclusions. For example, Chase, et al, 2000 performed a study of bird and small mammal community structure in CSS. They attempted to discover if the presence of specific birds and small mammals provides information about the overall species richness or composition in a given area. Using 37 species, they found the presences of specific species was not related to overall species richness, but in some cases, was related to the composition of species at a site. They also found the use of rare species as an indicator of species richness varied with geographical location and spatial scale. The lack of correlation between bird and mammal species richness led them to conclude that the use of a diverse suite of taxa may be a better method for conservation planning because it allows representation across the range of variation found in CSS. In addition, they found several of the bird species were sensitive to environmental changes. Birds such as the Cactus Wren, Sage Sparrow, Black-chinned Sparrow, and Rufous-crowned Sparrow were sensitive to habitat fragmentation.

The California gnatcatcher, an endangered CSS obligate, has also been studied to determine if it’s presence at a location is correlated with the presence of other species. Chase, et al, 1998, conducted a study to determine if the California gnatcatcher made a good indicator of species richness. In a two year study at 17 sites in Riverside, Orange and San Diego counties they found a very small correlation between presence of the California Gnatcatcher and species richness in one year and no correlation in the following year. As a result, they found that the California Gnatcatcher is not a “particularly good indicator of species richness in coastal sage scrub”.

Fleury, et al (1998), analyzed the effectiveness of reserves designed around a single umbrella species as a means of protecting a wide variety of plants and animals. Using 40 sensitive plant and animal species in the Otay Mesa region of San Diego, they found the gnatcatcher functioned as a suitable umbrella species for less than half of the species evaluated. Four criteria were used to place each species into one of three protection categories (good, marginal, poor). The criteria used included: 1) the presence of large unfragmented blocks habitat for a species within the reserve; 2) an abundance of at least several hundred individuals in the reserve; 3) at least 3 large blocks of habitat within an area and 4) the ability of an area to allow dispersal between sites. The best-protected species had area requirements that were equal to or less than the Gnatcatcher's with similar habitat requirements; primarily habitat generalists at lower trophic levels.

Besides having no empirical support, we find the indicator species approach unsatisfactory because it does not allow informed management decisions in many management situations. Simply knowing the presence of one species is associated with the presence of another may reduce the cost of monitoring, and may allow some level of informed decision-making in areas of land prioritization or reserve design. However, having an indicator species fails to allow insights into ecological processes controlling a system. For example, it does not indicate potential causes of decline for both the indicator and the target species (which could be different) and therefore does not allow effective management decisions in situations requiring information about species responses to extrinsic factors (i.e. some form of disturbance).

In terms of understanding overall ecosystem performance or health, the indicator species approach generally fails because species have specific and often complex responses to disturbance making it difficult for any one species to adequately predict the response of the entire system. Instead, studies have shown (Chase, et al, 2000) inferences are more likely using a mixture of species representative of the community being studied.

The Use of Avian Guilds as Indicators of Habitat Quality

A number of studies document the successful application of Avian-based IBI's in understanding and predicting the relative state of an ecosystem. Indeed, research done on birds is leading the way in converting IBI methods developed for freshwater streams to terrestrial landscapes. In general, these studies convince us of the utility in a guild-based, IBI approach to understanding system responses to disturbance. Here we briefly describe 6 studies using an IBI, or IBI-like approach, then discuss how a bird-based IBI for CSS might be structured.

Brooks and Croonquist 1990, and Croonquist and Brooks 1991. Here, the authors assigned all bird and mammal species in Pennsylvania values for response guilds that reflected sensitivity to disturbances (Brooks and Croonquist 1990). High guild scores represented birds and mammals with specific habitat requirements and therefore low tolerances to disturbance.

Croonquist and Brooks (1991) then sampled birds and mammals across 24 locations in two watersheds of central Pennsylvania and simultaneously estimated the degree of habitat alteration caused by human land use (agriculture, residential and commercial). Birds with high response guild scores decreased in abundance as the intensity of habitat alteration increased while the composition of mammal guilds showed no consistent pattern associated with habitat disturbance. Thus, specific guilds of birds were highly sensitive to habitat disturbance and could easily be tracked using this method. Interestingly, mammals were not impacted by disturbance. It is possible the large-scale nature of the research was too coarse to find a signal in small mammals, who respond to habitat disturbance at much smaller spatial scales than birds. This work showed that using the available, published information, such as foraging, breeding, functional characteristics, response and other attributes of birds will provide more insight into both the functional characteristics of an avian community and their subsequent response to disturbance than will similarity coefficients or simple estimates of species diversity. In other words, development of functional guilds will provide more valuable information than Shannon diversity or other more traditional techniques.

Brooks, et. al. In the late 1990's, Brooks et al. (1998) proposed a regional index of biological integrity and put forth six principles to guide the development of such an index. Their six principles are: "1) biological communities with high integrity are the desired endpoints; 2) indicators can have a biological, physical or chemical basis; 3) indicators should be tied to specific stressors that can be realistically managed; 4) linkages across geographic scales and ecosystems should be provided; 5) reference standards should be used to define target conditions; and 6) assessment protocols should be efficiently and rapidly applied." They found traditional measures of species richness and diversity were not sensitive to the stressors of management concern (invasive species, increased fragmentation, loss of habitat). At the same time, they determined it is not cost effective to collect detailed population, health or genetic data across many species of management concern across an entire region of a state.

Instead, they chose to develop response guilds and functional groups specifically to address the stressors of interest. They went on to empirically verify and document such a regional IBI in a forest riparian system by integrating four bioindicator communities (macroinvertebrates, amphibians, and avian communities and avian productivity of the Louisiana Waterthrush). These indicators are directly related to the ecological condition of associated habitats at one or more levels. Use of the Louisiana Water Thrush productivity, density and abundance acted as a bridge to the other three elements and spans the widest range of habitat scale. This bird is an area-sensitive species and as such may be used as a surrogate measure of the status of other species.

Bradford et al. Not all attempts to develop an IBI work to the level initially anticipated. For example, Bradford et al. (1998) demonstrated the application of an index of biological integrity in Great Basin rangelands in Idaho and Utah/Nevada using bird assemblages. They developed an IBI to understand and predict ecosystem responses to grazing in nonriparian rangeland. The metrics used were species richness, Shannon-Weaver diversity index, the percent of species considered shrub-obligate, total bird abundance, dominance by a single species, and relative abundance of individual species. Birds were sampled by point-count on 9 plots at 20 sites in each of 2 study areas, for a total of 360 plots. One study area consisted of sagebrush-steppe vegetation and the other area consisted of salt-desert shrub. Vegetation samples were taken at two predetermined points at each of the 9 plots. Data included location of nearest shrub, perennial grass, and perennial forb from the point, and then, species, distance from point to the main stem, canopy diameter, and maximum height. Percent cover for each of the three classes was also estimated. Unlike other attempts using birds in IBI's, the IBI here was not a strong indicator of rangeland habitat health in the intermediate stages of degradation; it could only distinguish between high and low levels of grazing.

Bradford et al, concluded the poor performance of the IBI was caused primarily by the low species diversity in the sagebrush (8 vs. 64-121 species forest studies mentioned herein) and the presence of a dominant avian species. They also suggested the relatively poor performance of bird metrics in sagebrush-steppe habitats may be caused by nonlinear relationships between vegetation characteristics and grazing practices and argued grazing affected shrub-obligate in ways other than those reflected in the vegetation variables measured. They concluded bird species assemblages can serve as indicators of the extremes in rangeland condition in the sagebrush-steppe habitats and perhaps can act as indicators of landscape-level effects on biological integrity resulting from human derived fragmentation.

Canterbury et al. Canterbury, et al. (2000)developed and tested community-level environmental indicators for monitoring forest bird populations and their associated habitat. Birds were grouped into three assemblages based on diet and foraging strategies, nesting location, and the common habitat used (described by canopy cover and tree basal area). They sampled 197 plots in loblolly-shortleaf pine forests from Georgia to Virginia for the number of bird species and the number of deciduous and coniferous stems in seven diameter categories. Bird species were also classified into four habitat assemblages grouped as disturbance-sensitive species (mature forest (MF) assemblage), disturbance-tolerant species (Shrubland (SL) and forest-edge (FE) assemblages), and neutral species (habitat generalist assemblages). The number of species in each of the three assemblages was counted at each plot to estimate the bird-community-index. In addition, a habitat index, based on levels of disturbance, was developed as a predictor of the bird-community index. The resulting bird-community index provided a broad-based indicator of how the bird-community responded to forest disturbance.

The bird-community index detected avifaunal responses to major human-created disturbances such as clearcutting and fragmentation occurring from forest conversion to agricultural and residential uses. The work showed a habitat index could be used as an independent measure of local disturbance affecting the bird community, and index values could be easily generated by relatively inexperienced field technicians.

O'Connell et al. In perhaps the best example of bird-IBI development, O'Connell, et al. (2000) categorized forest bird communities into eight mutually exclusive guilds based on behavior and responses to habitat disturbance. The response guilds were chosen to reflect different aspects of each species' breeding season life history traits. They included such items as trophic level and foraging behavior, whether resident or migratory, location of nests and nest placement, number of broods per season, and whether they are generalists or obligate forest species. Data on 112 total species was gathered from published literature and was used to assign the birds to 32 behavioral and physiological response guilds. This number was subsequently reduced to 16 guilds in 8 categories.

A reference gradient of ecological condition for 34 sites sampled in 1994 was established using best professional judgment and they were ranked in a three category scale of human disturbance. The scale went from pristine, to moderately disturbed to severely disturbed. A ranking of the same sites using only the bird community profile data was made. This information was used to develop a Bird Community Index (BCI), which was then used to rank forested areas in the central Appalachian Mountains into four broad categories; excellent, good, fair and poor. A second phase of research was then initiated to field verify the BCI. Here, birds and vegetation was sampled at 120 sites in a 168,420 square kilometer area. Samples were made at points along transects of up to 21 kilometers in length at separations of 50 to 200 m. Birds were sampled in 10 minute, unlimited-radius point counts along each transect. At each bird-sampling plot, a suite of vegetation variables was recorded. The variables included percentage herbaceous cover of graminoids, forbs, mosses, and ferns in three 5-meter radius subplots 15 meters away from the plot center. The percentage shrub cover in 3 categories was also recorded at each subplot as well as percent cover of the overstory trees.

O'Connell et al., used multiple regression analyses to discover landscape variables explaining variation in the BCI. A four-variable model consisting of landscape-level diversity (i.e. the amount of urbanization in a 1km radius around the plot), the percentage of forested land, canopy height, and slope best predicted the overall biotic integrity. The regression approach allows managers to develop a mechanistic understanding of the factors affecting the integrity of bird communities. In this case, the amount of urbanized land at fairly large scales, most impacted bird communities, which also showed natural levels of variation also explained by the amount and age of the forest, and slope. Overall, the BCI could reliably separate four categories of habitat quality. This work indicates a relatively inexpensive annual survey of birds can now effectively categorize forest habitat quality over large areas of Pennsylvania.

Developing a bird IBI for CSS.

Because so much is known about the natural history and response to disturbance in CSS birds, and other studies have successfully developed bird-based IBI's, we were able to develop a general, "working" framework for the development of an IBI for CSS birds. We emphasize our framework for IBI develop may change. Our upcoming field studies will verify/modify this framework and collect data on other species, which we will integrate to create a multi-species IBI. The approach described here for birds will be somewhat similar for all taxa.

Table 2 represents a proposed method for developing an IBI for birds in CSS (after O'Connell et al. 2000). In this approach, biological integrity is divided into three elements: function, composition, and structure. Function refers to particular processes occurring in an ecosystem or food web. As such, species are categorized in this element based on particular roles they carrying out within the ecosystem the occupy. In this case, we categorized species based on the role they play as predators. Composition refers to the actual assemblage of species in a system, and their origin (often times native vs. or exotic) relative to an intact example of the focal ecosystem. Finally, structure refers to how species making up the IBI use different structural characteristics of an ecosystem. The three elements are chosen based on an anticipated response to anthropogenic disturbance. Disturbance may impact any or all of the three elements. For example, Frequent fire will cause changes in the prey base of many predators, impacting the functional aspect of integrity while simultaneously impacting the presence or absence of exotic species (compositional element), and removing particular structural features of an ecosystem (i.e. shrubs for nesting or insect gleaning species).

Each Integrity Element has one or more Guild Categories and associated Response guilds (Table 2). Each guild is categorized as a specialist or generalist based upon their relationship to the specific elements of the ecosystem structure, function and composition. Response guilds are groups of species that are similar when categorized trophically, by origin relative to southern California, and by nesting or foraging habitat. The Trophic category includes omnivores; birds that are feeding generalists with neither plant nor animal food comprising less than one-third of their diet; and carnivores; birds that generally eat invertebrates and vertebrates for more than one-half their diet. The carnivores are subdivided into groupings associated with where they feed in the vertical dimension. Origin levels represent the basic origin of the bird. Exotics we define as birds not normally found in CSS. This includes birds found in human-modified habitats, such as edge specialists. Resident birds use CSS on a year-round basis, not just in the breeding season, while migratory birds use CSS seasonally. Nest placement is for the two major nesting methods, ground and shrubs, which is typical of

CSS. Primary habitat is based upon the breeding habitat for resident birds and the foraging habitat for all others.

The metric ratings of 5, 3, and 1 are categorical representations of deviations from a relatively undisturbed CSS habitat. The value 5 indicates a guild is within the range found in undisturbed CSS: 3 indicate some deviations, and 1 deviates strongly from an undisturbed or reference CSS habitat. The sum of all metrics taken over all the sample plots within a site provides a measure of the integrity of the habitat at that site (Brooks and Croonquist 1990, Croonquist and Brooks 1991, O'Connell et al. 2000). The aggregate of scores from all sites gives a measure of the health of the total CSS habitat within a study area.

Table 2, Potential Avian Guild Attributes for Measuring CSS Habitat Disturbance*

Integrity Element	Guild Category	Response Guild (%)	Specialist	Generalist	Metric Rating		
					5	3	1
Functional	trophic	omnivore		x			
		carnivore, bark prober	x				
		carnivore, ground gleaner	x				
		carnivore, foliage gleaner	x				
Compositional	origin	Exotic		x			
		resident	x				
		migratory		x			
Structural	nest placement	Shrub nester	x				
		ground nester	x				
	primary habitat	CSS generalist		x			
		CSS obligate	x				

*Adapted from O'Connell et al. 2000, Croonquist & Brooks 1991, and Karr 1991. Metric scoring to be determined.

Guild data for coastal sage scrub candidate avifauna are provided in Table 3. We expect to find each species in the table within or near CSS sampling locations. Some species are more associated directly with CSS while others accommodate fragmented patches and edges, while still others accommodate suburban areas surrounding CSS, and finally, some breed in chaparral or riparian areas but forage within CSS. The birds listed on the Primary and Secondary Species list in the draft Coastal Scrub and Chaparral Conservation Plan (Lovio 2000) will certainly be on the final list.

The avifauna of Table 3 are listed again in Table 4, but assigned to one of the 11 possible guilds possible in Table 2. We consider the guild assignments in Table 4 preliminary and will verify these categories with local experts. However, based on these categories, we see that for each of the 11 possible guilds, the maximum number of species possible varies from X – X. We emphasize a site does not need to have the maximum number of species in a category to receive a 5, but instead, it must within natural levels of variation, close to the number of species found in undisturbed sites.

Table 3, Guild Data for Candidate Avifauna in Coastal Sage Scrub and Environs

Common Name	Habitat	Diet	Foraging Substrate	Foraging Technique	Nest Site	Residence
Cooper's Hawk	Mature forest, open woodlands, wood edges, river groves	Mostly birds & small mammals.	Air, ground.	Aerial pursuit.	In tree @ 25-50 ft.	Mig. Sp – F.
Red-tailed Hawk	Open country, woodlands, prairie groves, mountains, plains, roadsides.	Mammals, some birds and reptiles.	Ground	High patrol, swoops.	In trees, cliff ledges towers, etc. @ up 120 ft.	Res.
California Quail	Broken chaparral, woodland edges, coastal sage scrub, parks, farms.	Mostly seeds & leaves, some berries, flowers, arthropods.	Ground	Ground glean.	On ground under cover.	Res.
Mourning Dove	Farms, towns, open woods, roadsides, grasslands, edges.	Seeds	Ground	Ground gleans, foliage.	In shrubs and on ground.	Res.
Greater Roadrunner	Deserts, open country with scattered brush	Arthropods, reptiles, rodents, birds.	Ground	Ground Glean	Dense bush or low tree or cactus.	Res.
Lesser Nighthawk	Arid scrub, dry grassland, desert washes	Flying arthropods.	Air	Aerial foraging.	On level ground.	Mig. Sp – F..
Common Poorwill	Dry hills, open brush, chaparral.	Flying arthropods.	Air	Hover and glean.	On ground.	Res. (?)
Black-chinned Hummingbird	Semi-arid country, river groves, chaparral, suburbs.	Nectar, arthropods.	Air	Hover and glean, hawk.	Tree or shrub.	Mig. Sp – F.
Anna's Hummingbird	Gardens, chaparral, open woods.	Nectar, arthropods.	Air	Hover and glean, hawk.	On tree branch.	Res.
Costa's Hummingbird	Deserts, washes, mesas, sage scrub, arid hillsides.	Nectar.	Air	Hover and glean.	Sparsely leaved shrub.	Mig. Sp – F.
Pacific Slope Flycatcher	Moist woods, mixed forests, shady canyons	Arthropods.	Air	Hawk, hover and glean.	In trees near ground.	Mig. Sp – F.
Black Phoebe	Shady streams, walled canyons, farmlands, towns;	Arthropods.	Air	Hawk, hover and glean.	Mud nests on cliffs, bridge supports, etc.	Res.

	near water.					
Say’s Phoebe	Scrub, canyons, ranches, open areas.	Arthropods.	Air	Hawk, hover and glean.	Rocky ledge or crevices in cliffs.	Res.
Ash-throated Flycatcher	Semi-arid country, deserts, brush, mesquite, pinyon-juniper, dry open woods.	Arthropods, some berries.	Air	Hawk, hover and glean.	Cavities.	Mig. Sp - F.
Cassin’s Kingbird	Semi-open high country, pine-oak mountains, groves.	Arthropods, some berries.	Air, ground	Hawk, hover and pounce.	In large tree.	Mig. Sp - F.
Western Kingbird	Semi-open country, farms, roadsides, towns.	Arthropods, some berries.	Air, ground	Hawk, hover and pounce.	In tree, 15-30 feet.	Mig. Sp - F.
Cliff Swallow	Open to semi-open land, farms, cliffs, river bluffs, lakes.	Arthropods.	Air	Aerial foraging.	On vertical surface with overhang.	Mig. Sp - F.
Western Scrub Jay	Foothills, oak-chaparral, river woods, pinions, junipers, suburbs.	Omnivorous.	Ground	Ground glean.	Low in tree or shrub.	Res.
Bushtit	Oak scrub, chaparral, mixed woods, pinions, junipers.	Arthropods, some berries.	Foliage, bark	Foliage, bark glean.	Tree or shrub.	Res.
House Wren	Open woods, thickets, towns, gardens.	Arthropods.	Ground, foliage.	Ground, foliage glean.	Cavities.	Mig. Sp - F.
Bewick’s Wren	Thickets, underbrush, chaparral, gardens.	Arthropods, some berries.	Ground, foliage.	Ground, foliage glean.	Cavities.	Res.

Table 3, Cont., Guild Data for Candidate Avifauna in Coastal Sage Scrub and Environs.

Common Name	Habitat	Diet	Foraging Substrate	Foraging Technique	Nest Site	Residence
Canyon Wren	Cliffs, canyons, rockslides, stone buildings, boulder fields.	Arthropods.	Ground, foliage.	Ground, foliage glean.	Hole or crevice in rocks.	Res.
Cactus Wren	Chollas, prickly pear @ <450 m elev.	Arthropods, some fruits and seeds.	Ground, foliage.	Ground, foliage glean.	Hole in cactus.	Res.
Wrentit	Dense chaparral, coastal sage, parks, garden shrubs.	Arthropods and berries.	Foliage, bark.	Foliage, bark glean.	Dense, low shrub.	Res.
California Gnatcatcher	Low elevation coastal sage scrub with broken canopy.	Arthropods.	Foliage, air.	Foliage glean, hover and glean.	Dense, low shrub.	Res.
Northern Mockingbird	Dense, low shrubs and open ground, towns, farms, roadsides, thickets, brushy areas.	Arthropods and berries.	Ground, foliage.	Ground, foliage glean.	Dense shrub or tree.	Res.
California Thrasher	Chaparral, foothills, valley thickets, parks, gardens.	Arthropods and berries.	Ground, foliage.	Digging, foliage glean.	Dense shrub or thicket.	Res.
Orange-crowned Warbler	Brushy clearings, chaparral, aspens, undergrowth.	Arthropods, some berries.	Foliage	Foliage glean.	On ground under overhanging vegetation.	Mig. Sp - F.
Common Yellowthroat	Swamps, marshes, wet thickets, edges.	Arthropods. few seeds.	Foliage, air.	Hover glean, bark glean.	Low on tussocks of briers, weeds, grasses.	Mig. Sp - F.
Black-headed Grosbeak	Deciduous and mixed woods.	Arthropods, seeds, and berries.	Foliage.	Foliage glean.	In tree or large shrub.	Mig. Sp - F.
California Towhee	Brushy areas, chaparral, coastal sage scrub.	Seeds and arthropods.	Ground	Ground glean.	In dense shrub.	Res.
White-crowned Sparrow	Thickets, chaparral, gardens, parks.	Arthropods and seeds.	Ground, foliage.	Ground, foliage glean, hawks.	On ground or in shrubs.	Res.
Bell's Sage Sparrow	Dry brushy foothills, semi-open, evenly	Seeds and arthropods.	Ground, foliage.	Ground, foliage glean.	Low shrub.	Res.

	spaced chaparral, coastal sage.					
Black-chinned Sparrow	Brushy mountain slopes, open chaparral, sagebrush.	Seeds and arthropods.	Ground, foliage.	Ground, foliage glean.	Low shrub.	Mig. Sp - F.
Rufous-crowned Sparrow	Grassy or rocky slopes with sparse low bushes, chaparral, coastal sage scrub, drier, moderate to steep slopes.	Arthropods and seeds.	Ground, foliage.	Ground, foliage glean.	On ground at base of bush or grass clump.	Res.
Song Sparrow	Thickets, brush, marshes, roadsides, gardens.	Arthropods and seeds.	Ground, foliage	Ground, foliage glean.	On ground under clump of trees.	Res.
Western Meadowlark	Open fields, pastures, meadows, prairies.	Arthropods and seeds.	Ground	Ground glean.	On ground in dense grass.	Mig. Sp - F.
Brown-headed Cowbird	Farms, fields, prairies, wood edges, river groves.	Seeds and arthropods.	Ground	Ground glean.	Parasite.	Res.
Hooded Oriole	Open woods, shade trees, palms.	Arthropods, berries, nectar.	Foliage	Foliage glean.	In palm or yucca.	Mig. Sp - F.
House Finch	Cities, suburbs, farms, canyons, semi-open chaparral and brush.	Seeds, buds, berries.	Ground, foliage	Ground, foliage glean.	Wide variety of sites.	Res.
Lesser Goldfinch	Open brushy country, open woods, gardens.	Seeds, some arthropods.	Foliage	Foliage glean.	Vertical fork of tree or shrub.	Res.

Table 4 Preliminary Guild Assignments for CSS Candidate Avifauna

Common Name	Scientific Name	Probable Guild**										
		1	2	3	4	5	6	7	8	9	10	11
Cooper's Hawk	*Accipiter cooperii*											
Red-tailed Hawk	*Buteo jamaicensis*											
California Quail	*Callipepla californica*											
Mourning Dove	*Zenaida macroura*											
Greater Roadrunner	*Geococcyx californianus*											
Lesser Nighthawk	*Chordeiles acutipennis*											
Common Poorwill	*Phalaenopitlus nutallii*											
Black-chinned Hummingbird	*Archilochus alexandri*											
Anna's Hummingbird	*Calypte anna*											
Costa's Hummingbird	*Calypte costae*											
Pacific Slope Flycatcher	*Empidonax difficilis*											
Black Phoebe	*Sayornis nigricans*											
Say's Phoebe	*Sayornis saya*											
Ash-throated Flycatcher	*Myiarchus cinerascens*											
Cassin's Kingbird	*Tyrannus vociferans*											
Western Kingbird	*Tyrannus verticalis*											
Cliff Swallow	*Hirundo pyrrhonota*											
Western Scrub Jay	*Aphelocoma californica*											
Bushtit	*Psaltriparus minimus*											
House Wren	*Troglodytes aedon*											
Bewick's Wren	*Thryomanes bewickii*											
Canyon Wren	*Catherpes mexicanus*											
Cactus Wren	*Campylorhynchus brunneicapillus*											
Wrentit	*Chamaea fasciata*											
California Gnatcatcher	*Polioptila californica*											
Northern Mockingbird	*Mimus polyglottos*											
California Thrasher	*Toxostoma redivivum*											
Orange-crowned Warbler	*Vermivora celata*											
Common Yellowthroat	*Geothlypis trichas*											
Black-headed Grosbeak	*Pheucticus melanocephalus*											
California Towhee	*Pipilo crissalis*											
White-crowned Sparrow	*Zonotrichia leucophrys*											

Bell’s Sage Sparrow	*Amphispiza belli*											
Black-chinned Sparrow	*Spizella atrogularis*											
Rufous-crowned Sparrow	*Aimophila ruficeps*											
Song Sparrow	*Melospiza milodia*											
Western Meadowlark	*Sturnella neglecta*											
Brown-headed Cowbird	*Molothrus ater*											
Hooded Oriole	*Icterus cucullatus*											
House Finch	*Carpodacus mexicanus*											
Lesser Goldfinch	*Carduelis psaltria*											

*Most common bird species as specified by the respective authors. Includes edges and adjacent urban areas.
**1 = omnivore, 2 = bark prober, 3 = ground gleaner, 4 = foliage gleaner, 5 = exotic, 6 = resident, 7 = migratory, 8 = shrub nester, 9 = ground nester, 10 = CSS generalist, 11 = CSS obligate

Data Gaps and Recommendations for further research

While some avian data provides insight into the health of forested habitats and rangeland habitats, no such high quality research provides these types of data for CSS habitats. In particular, no information exists connecting avian presence or absence with an indication of CSS habitat health or disturbance. Though we expect to accomplish much of the work necessary to measure or predict CSS habitat health; long-term data will be required to understand how avian guilds and individual species respond to changes in CSS disturbance and how these various interactions affect the presence and absence of guilds. Once the interaction between disturbance and bird communities are better understood, we will be able to refine the IBI tools available to managers for making informed conservation decisions.

Herpetofauna

Introduction

Amphibian and reptile species should be useful indicators of human mediated disturbance in CSS for three primary reasons. 1) As a group, amphibians and reptiles respond to a variety of anthropogenic disturbance. The rich diversity of life history patterns, body forms, and behaviors displayed by the herpetofauna of S. CA virtually ensures that no disturbance can proceed without ultimately eliciting a response from some component of the community. 2) Amphibians and reptiles play significant ecological roles in both terrestrial and aquatic ecosystems. In terrestrial ecosystems amphibians and reptiles are the primary vertebrate predators on invertebrates as well as the primary prey base for a number of bird and mammal species. This unique trophic position makes them a major “conveyor belt” for invertebrate energy sources to predatory animals higher up the food chain (Stebbins and Cohen 1995). In addition, in many terrestrial ecosystems the herpetofaunal community makes up a large part of the vertebrate biomass. With twenty-five fold greater conversion efficiencies (the proportion of the energy consumed that is converted to new animal tissue) than birds and mammals, amphibians and reptiles populations are able to reach and sustain much greater densities than their endothermic counterparts (Pough 1980, 1983). Because this ability to sustain high population densities even when overall ecosystem resources are low, ectotherm populations are able to act as energy reserves for other predators present in the system (Stebbins and Cohen 1995). 3) Detecting herpetofaunal response to disturbance is facilitated by amphibians’ and reptiles’ tendencies to be long lived and to maintain relatively stable population densities through time.

We initially used electronic search engines and species names of the S. CA herpetofauna, as well as different forms of disturbance to initiate the searches. Unfortunately, the lack of published work on CSS herpetofauna became readily apparent. Given the lack of studies on CSS herpetofauna, we chose to make inferences concerning how the local CSS herpetofaunal community may respond to anthropogenic disturbance by looking at trends and associations documented outside S. CA. Even though this situation is not ideal, we believe some significant insights came from the literature review. However, we feel analyses of data collected by Dr. Robert Fisher will build a strong understanding of herpetofaunal responses to disturbance. We summarize our findings of herpetofaunal response to different forms of disturbance in Table 1.

Amphibians

Amphibians are sensitive to changes in landscape structure, the presence of introduced aquatic predators, and exposure to atmospheric pollutants (see references cited in table 1). Included within the category “landscape structure” are a number of studies that document amphibian sensitivity to differences in habitat patch size and isolation, road density, and wetland permanency. Amphibians’ significant response to differences in road densities makes intuitive sense when considering amphibian biology. Because many amphibians breed, forage, and overwinter in more than one habitat, these species must make seasonal movements to and from different habitat types. When these movements occur across roads, mortality can be substantial (Fahrig et al. 1995). In Hels and Buchwald (2001), the authors estimated that roughly ten percent of a local adult population (which represents individuals from all ponds located within 250 meters of the road) of common spadefoot toads (Pelobates fuscus) and brown frogs (Rana temporaria and Rana arvalis) were killed annually by vehicular traffic over a five-year period.

Amphibians' negative association with permanent wetlands is likely due to the presence of exotic predators in these systems. Permanent wetlands (perennial streams, reservoirs, and ponds) typically harbor a greater number of exotics predators and competitors than the more ephemeral aquatic habitats (Adams 2000). Because native amphibian populations are significantly impacted by predation from introduced fish, bullfrogs, and crayfish, and by competition from introduced bullfrog larvae (Gamradt and Kats 1996; Lawler 1999; Goodsell and Kats 1999; Knapp and Matthews 2000; Kiesecker et al. 2001) it becomes obvious why there is a negative correlation between exotic predator and competitor presence and native amphibian abundance. In one clear example of this relationship, Fisher and Shaffer (1996), using broad-scale field sampling and historical analyses of museum records to quantify amphibian declines in California's Great Central Valley, documented a strong correlation between the presence of introduced predators and the absence of native amphibian species. Throughout the surveyed regions native amphibians were found more frequently at higher elevations while exotic species were found primarily in lowland areas. Evidence exists for some of the native species that suggests their present distributions represent a significant restriction to higher elevation sites from a formerly broader distribution.

Amphibians are sensitive to atmospheric pollutants present in biological systems (references cited in Stebbins and Cohen 1995; Read 1998; Marco et al. 1999; Davidson et al. 2001). Specific aspects of amphibian biology that might explain why amphibians are likely more susceptible to the presence of chemical pollution than any other vertebrate group are: (1) adult amphibians feed primarily on small invertebrate animals, making them susceptible to the effects of biomagnification of chemical contaminants in the food web; (2) amphibian larvae are susceptible to the deleterious effects of ingesting and absorbing chemicals easily transported and accumulated in aquatic mediums; (3) amphibian adults, larvae, and eggs all posses absorptive surfaces designed to be permeable to gases and liquids, the basic nature of which facilitates the absorption of chemical contaminates present in the system (Stebbins and Cohen 1995). To some researchers, the evidence of amphibian sensitivity and opportunity for exposure to chemical contaminants is so great they have suggested that chemical pollution may be the single most important factor contributing to present day worldwide amphibian declines (Stebbins and Cohen 1995).

Reptiles

Reptiles, specifically lizards, snakes, and turtles, respond to changes in land use, fire history, and landscape structure (Table 1). For lizard species, studies have documented significant effects of logging, grazing, agricultural activity, mining, human recreation and wildfire. Across this diverse suite of disturbance types, the one common element is the disturbances' shared tendency to simplify microhabitat structural and compositional diversity. Because lizard species exhibit extensive habitat specificity in natural systems, reducing a habitat's natural heterogeneity will significantly impact lizard species dependent upon the specific microhabitats eliminated by the disturbance (Pianka 1989). This microhabitat simplification eliminates critical habitat components necessary for lizards to carry out their most basic biological activities such as, thermo-regulation, predator avoidance, breeding activities, and juvenile dispersal (Hecnar and M'Closkey 1998; Germaine and Wakeling 2001). As evidence of this phenomenon, two studies conducted in Australia's Eucalyptus forests, document that changes to forest understory density, amount of woody litter, percent shrub cover, and structural heterogeneity all contribute significantly to explaining patterns of lizard abundance and species richness (Smith et al., 1996; Brown 2001).

For snakes, a few studies suggest they are sensitive to changes in patch size, road density, human recreation, and fire history. In one study, snake diversity was shown to decrease with decreasing patch size (Kjoss and Litvaitus, 2001). In support of these findings, preliminary analyses of data collected from ongoing S. CA herpetofauna surveys identify a suite of snakes species believed to be sensitive to the effects of habitat fragmentation (Fisher and Case, 2000; R.N.F. unpublished data). In both cases the underlying causes of sensitivity are unknown, however, the incidence of road mortality in snakes has been documented by a number of studies (Rosen and Lowe 1994; Bernardino and Daryrumple 1992; Klauber 1931, 1939) and increases in road density in fragmented landscapes are assumed to significantly impact a number of snake populations (Greene 1997). Because of the difficulty in estimating snake populations densities, good quantitative estimates of the impact road mortality has on local snake populations is rare. In one of the few good examples, Rosen and Lowe (1994) estimated highway mortality for snakes encountered during four years of sampling along a 45km stretch of highway in the Sonoran Desert of southern Arizona. The authors estimated the highway mortality was equivalent to the removal of five square kilometers of snake populations from the surrounding region. Additionally, the authors noted the number of snakes observed on the roads during the survey was an order of magnitude less than the number of snakes observed decades earlier by surveys conducted along the same stretch of road.

The effect of fire on local snake populations has rarely been studied (table 1.) and with mixed results. However, generally it does appear snake species favoring more open habitats are found in greater densities following fires, while more secretive species and those using ambush predatory tactics are more negatively impacted (Smith et al., 2001).

Freshwater turtle populations appear sensitive to increases in human activity in areas surrounding their streamside habitats (Garber and Burger 1995). Direct removal, road kills, handling by recreationists, increased predation, and disturbance by dogs are impacts typically association with increased human use of surrounding upland areas. In one clear example of this relationship, the decline of North American wood turtles (Clemmys insculpta) in a southern New England wildlife reserve was inextricably linked to increases in the use of the reserve for human recreation (primarily fishing and hiking). Previous to the reserve being opened to human recreational use, the turtle populations in the reserve remained stable. With the commencement of human recreational use, the turtle populations in the reserve decreased steadily over a ten-year period (declining by nearly 100% in ten years). During the decline, the turtle populations experienced recruitment failure and a disproportionate loss of females from the populations (Garber and Burger, 1995).

In a similar situation, ongoing mark-recapture studies of a southwestern pond turtle (Clemmys marmorata) population in the Sacramento Valley of California have documented recruitment failure and a disproportionate loss of females from the population (Phil Spinks and H. Bradley Shaffer, unpublished data). As in case described above, this population appears to be sensitive to increases in human activities in the surrounding terrestrial landscape that have occurred over the last few decades. In both turtle studies, the sensitivity of female turtles to disturbance is believed to be due to their increased vulnerability while moving through upland areas in search of appropriate sites to deposit their eggs.

Conclusion

Based on the findings of the reviewed published literature, it appears likely that measuring local CSS amphibian and reptile populations will provide insight into the types and levels of disturbance that occur within CSS ecosystems. Specifically, measuring local amphibian abundance is likely to provide researchers with insight into changes to local landscape structure. As local aquatic-breeding amphibians (i.e. western toad (Bufo boreas), western spadefoot toad (Spea hammondii), and California newt (Taricha torosa)) make seasonal movements through the surrounding habitat matrix, disturbances that fragment and alter this landscape will surely be reflected in changes to their local population densities.

Measuring the presence or absence of introduced aquatic predators (i.e. bullfrog (Rana catesbiana), mosquito fish (Gambelia spp.), and crayfish) will provide insight into the health and productivity of freshwater habitats for native CSS amphibian species such as the California treefrog (Hyla cadaverina) and the arroyo toad (Bufo californicus) and other native freshwater species. Likewise, severe and sudden declines or unexplained absences of even the most common CSS amphibian species may be indicative of chemical contamination occurring with the system.

Measurements of the local CSS lizard diversity and abundance, specifically the abundance of species with specific habitat requirements like western whiptail lizards (Cnemidophorus tigris), Gilbert’s skinks (Eumeces gilberti), coast horned lizards (Phrynosoma coronatum), and banded geckos (Coleonyx variagatus), should provide researchers with insight into recent land use history. Lizard diversity appears to be a good metric for measuring changes to a local landscape’s microhabitat structural and compositional diversity. Monitoring changes to the local abundance of highly active wide-ranging CSS snake species, such as the coachwhip snake, Masticophis flagellum, will provide researchers with information concerning changes in road densities in the local region. Lastly, the abundance, sex ratio, and age structure of southwestern pond turtle populations should provide insight into the level of human activity occurring within surrounding upland habitats.

In sum, because amphibians and reptiles respond to a variety of disturbances, play critical ecological roles in both terrestrial and aquatic systems, and maintain relatively stable population densities through time, these species and species assemblages should be considered as significant candidates for inclusion in any IBI.

Data gaps and recommendations for future research

In general, the lack of published information on CSS herpetofauna makes predicting responses to disturbance difficult. As mentioned above, we strongly feel the work by Dr. Fisher will greatly increase our understanding of the CSS herpetofauna on a number of fronts. His large-scale, long-term monitoring program will allow us to address questions ranging from the evolutionary history and genetic structure of focal species, to how individiduals, populations and communities respond to disturbance.

Arthropods

Introduction

Conservation efforts for arthropods are often problematic. Although the species diversity and overall biomass are excessively high, suitable taxonomic information is often unavailable (Kim 1993). This lack of information is worsening due to the increasing shortage of taxonomic expertise. Arthropods have also been traditionally thought of as nuisances and have a negative public perception (Kim 1993). These factors have all contributed to a disproportionately low occurrence of arthropods in conservation planning (McNaughton 1989, Hafernik 1992). For example, of the 290 species listed as threatened or endangered in California, only 21 (~7%) are arthropods (Table 5). California has an additional designation of “fully protected species” which conspicuously lacks a category for invertebrates or arthropods. This is also true for the species of special concern. Finally, the Multi Species Conservation Plan for San Diego only included two species of arthropods (Saltmarsh skipper – *Panoquina errans* and Thorne’s hairstreak – *Mitoura thornei*). There is no suitable justification for the lack of consideration of California’s arthropods, and it should be considered a high priority for future research and conservation.

Arthropods as Indicators of biological condition

The majority of research we reviewed focused on the use of arthropods as bioindicators. Some researchers argue arthropods are potentially better surrogate species (indicators) for monitoring ecological problems than other taxonomic groups based on a number of characteristics (Kremen et al. 1993, Kimberling et al. 2001). They exhibit relatively high species diversity, endemism, and encompass the geographic range of interest. They also show a wide range of life histories, tolerances to perturbations, and ecological specialization. Furthermore, because of their small size, they can be used in monitoring plans for fragmented areas no longer supporting vertebrate indicator species (Kremen et al. 1993). Indeed, due to their overwhelming diversity and abundance, arthropods are considered an untapped source for conservation planning and management (Kim 1993, Kremen et al. 1993, McGeoch 1998)

Small species have been more successful as indicators of ecosystem health than larger species for a number of reasons (Siemann and Haarstad 1996). First, smaller species show a rapid uptake of environmental contaminants (Walker 1983). Second, they have rapid generation times, allowing for rapid responses to habitat change (Caro 1999) since the juvenile life stages are more at risk to environmental degradation (Blus et al. 1974). Finally, mobile species provide information at the landscape level where the small ground obligate species show a more localized response (Caro 1999).

To date, arthropods have been successfully incorporated into IBI's in numerous aquatic systems and in one terrestrial system. Many recent studies have considered the potential of invertebrates as reliable indicators of disturbance or degradation in terrestrial systems. An IBI approach was adapted to terrestrial systems by focusing on arthropods at the Department of Energy Hanford site in Washington (Kimberling et al. 2001). They observed patterns in species richness along disturbance gradients with the following groups: *Diptera, Tachinidae (Diptera), Acarina, Tenebrionidae (Coleoptera)*, parasitoids, decomposers, and predators. The relative abundance of *Eleodes (Tenebrionidae)* decreased and dominance increased along the gradient. Their integration of these measures into an index provided an effective measure of relative biological condition useful in evaluating site restoration. Thus previous studies suggest the use of arthropods as components of IBI's is feasible and yields productive results.

There are several difficulties inherent in using arthropods in a multi-species monitoring plan. These problems revolve around the tremendous diversity seen in arthropods and the difficulties in sorting and identifying species. Thus, this diversity requires a focused and structured approach to inventory and monitoring (New 1999). One approach to these problems involves first defining the goals and criteria necessary for a surrogate species, and performing a pilot study to validate the choice (Caro 1999). This method reduces the total number of species used in the study greatly reducing logistic and monetary constraints. Another approach useful in large- scale monitoring efforts is the use of morphospecies (Oliver 1996). This also reduces both the time and cost. However, given the potential for high endemism and rare species, we recommend full identification to species whenever possible in the initial phases of arthropod monitoring and IBI development. Based in part of the observed levels of endemism, Redak (2000) estimated the true number of threatened or endangered arthropods is at least an order of magnitude larger than the current number listed. Thus, the use of just morphospecies, without additional taxonomic separation, will likely mask the true diversity in a system.

Existing Ecological information

Arthropod surveys within coastal sage scrub (CSS) in San Diego County have occurred, with one of the more comprehensive single-site reports from Point Loma (Bruyea 1994). Unfortunately, these types of surveys generally have little information or recommendations for conservation. Recent work focused on an inventory and analysis of arthropods coupled with conservation implications and/or recommendations. Of key importance to the investigation of arthropods and CSS is identifying a response to anthropogenic changes in the landscape (fragmentation, isolation, patch size, edge effects, reserve design, overgrazing, introduced species, and fire). Here we first discuss general ecological knowledge and arthropod responses to disturbance for main taxonomic groups. We then briefly describe the role arthropods play in CSS food webs. Finally we summarize a handful of studies showing more general responses of all arthropods to fire, mechanical disturbance, and habitat fragmentation.

Ants

There are approximately 200 species of ants identified from California (Powell and Hogue 1979). Some of the major invasive species in California include the red imported fire ant (*Solenopsis invicta*), the Argentine ant (*Iridomyrmex humilis*), the Pharaoh ant (*Monomorium pharaonis*) and the pavement ant (*Tetramorium caespitum*), with a continuing expansion of their distribution within the state (Knight and Rust 1990). Suarez et al. (1998) and Suarez el al. (2002) investigated the influence of habitat fragmentation and exotic ant invasion on native ants in CSS patches in San Diego County. Greater times since isolation, smaller fragment sizes, patches with relatively more edge, and higher percent native vegetation, were all positively correlated with the relative abundance of exotic Argentine ants. They also found the abundance of argentine ants, fragment size, and time since isolation most strongly influenced the presence of native ants.

Beetles

The families Carabidae (predatory ground beetles) and Tenebrionidae (darkling ground beetles) contain over 800 and 400 species throughout California, respectively (Powell and Hogue 1979). The beetles lack wings, and live on the ground or in burrows, making them ideal for pitfall trapping and potential indicators of land use, fragmentation, disturbance, and change (Luff and Rushton 1988, Luff and Woiwod 1995). Also, biogeographic investigations into fragmented dune systems indicated the distribution of sand-obligate beetles was nested, resulting from isolation and fragmentation of their habitat (Rahn and Rust 2000).

The Carabid beetles are well studied across many regions of the globe with regards to their application for environmental studies and conservation (Stork 1990). Carabids and Tenebrionids may be extremely useful species in an IBI because they are reasonably understood in California, and the numerous species are both widespread and narrowly distributed. By focusing on the beetles that are flightless, with either reduced or absent wings, the impact of fragmentation and isolation should be seen through the resulting assemblage of these species found at each study site.

Although many studies indiciate beetles show a response to natural and anthropogenic alterations, only a few studies have occurred on this group of arthropods in CSS (Bolger 2000). A comprehensive assessment of the beetles of San Diego County was conducted, which may provide insight into changes in species richness over the past several decades (Moore 1937). There have also been taxonomic studies on the Coleoptera of Baja, California (Horn 1894) along with an assessment of the genus *Eleodes* (Triplehorn 1996).

Butterflies/moths

Approximately 240 species of butterflies are identified in California; with well over 3,000 species of moths and many others not yet described (Powell and Hogue 1979). Some consider them suitable bio-indicators given their sensitivity to micro-climate and light level changes, and their interactions with plants (Kremen 1992). Brown (1997) discussed the use of arthropods as indicators or "early warning' systems based on their short lifecycle characteristics. In this study, butterflies responded well as indicators of environmental heterogeneity, species richness, and (natural) disturbances. Butterfly populations responded best to levels of disturbance near the natural levels, with both species and genetic diversity being lower at unnatural levels of disturbance (Brown 1997). In his examination of the ability to use California gnatcatchers as an umbrella species for 2 butterflies and 1 moth, Rubinoff (2001) found that the presence of arthropods in CSS was dependent on fragment size, whereas gnatcatcher distribution was independent of patch size. All 3 arthropods were specialist feeders on *Eriogonom fasciculatum*, a common CSS plant, and the arthropods' limited mobility allowed for a conservative estimate of habitat fragmentation effects on invertebrates.

Spiders

There are multiple compilations of described spider species from California, with estimates from 150 to 1,029 (see (Prentice et al. 2001) for a complete description). The most comprehensive inventories of spiders in CSS habitats in S.CA has revealed 200 species; 35 of which were new records for the county, 4 were new records for the state, 20 were undescribed, and 7 were non-native (Prentice et al. 2001). Other studies of CSS communities in San Diego County suggest non-native spiders have no significant influence on the native ground-dwelling species, with the productive lowland coastal region having both the highest number of invasive spiders and the highest number of spider species overall (Burger et al. 2001). The authors also suggest the impact of non-native spiders on the local community is largely dependant on the availability of resources. The highly linked CSS communities typically had more invasive species, but their higher diversity and resource availability increased their resistance to the deleterious impacts of exotic spiders.

The role of Arthropod in CSS food webs

Arthropods as prey items

A few studies suggest arthropods play critical roles in the CSS food web. If so, the presence or absence of arthropods with trophic links to other taxa within the food web could be a major component of an IBI. Surveys suggest arthropods may play a key role in determining habitat quality of insectivorous birds (Burger et al. 1996). For example, the habitat of California gnatcatchers was not associated with vegetation type, but rather with food abundance and diversity (Redak et al. 1996), primarily, leafhoppers (*Homoptera*) and spiders (*Araneae*), with a lesser dependence on true bugs (*Hemiptera*) and wasps, bees, and ants (*Hymenoptera*) (Burger et al. 1999). Recently, work by Ted Case and Andrew Suarez shows strong evidence for cascading impacts of argentine ants through the CSS food web (Suarez and Case 2002). Their work shows argentine ants reduce populations of native ants and result in declines in horned lizards, a predator specializing on native ants.

Pollination

There are 80 species of bees, 7 beetles, 3 butterflies, 10 muscoid flies, 4 syrphid flies, 7 beeflies, 7 wasps, and 1 sphyngid moth identified as pollinators of CSS vegetation (Moldenka 1976). There is often an important link between these arthropods and the multitude of host plants, rare and endemic plants, and endangered plants. The unique flora of southern California has led to a high number of mutualistic relationships between plants and arthropods; of the 1,200 native bee species, almost 800 are considered specialists (with 172 species identified in coastal dunes and sage, and 520 species identified in the S. CA coastal ranges, Moldenka 1976). The insect pollinators also provide a substantial economic service for California's agricultural economy. The introduction of the numerous non-native species on the pollinators is not well understood. However, the introduced honey bee (*Apis mellifera*) is now integrated into the pollination biology of California plants, and has potentially caused the extirpation or extinction of many native species of insect pollinators (Moldenka 1976).

Responses to disturbance

Coastal Sage Scrub Fire Ecology and Arthropods

A tremendous amount of work has been done on the response of the chaparral and CSS community to fire. However, post-fire arthropod succession is less understood. In chaparral, the arthropod community follows predictable patterns related to the succession of plants, suggesting the initial phase of arthropod succession is largely influenced by the presence of plants, while later succession is influenced by the presence of other arthropods (Force 1981). Pollen/nectar feeders and predatory species can be abundant the spring after the fire, while other feeders and parasitic arthropods colonize later (Force 1982).

Depending on the type of ecosystem, fire may be influential on many species but may not be necessarily harmful (Samways 1994). In fact, some species are dependent on a regular fire regime. Some species of beetles have developed highly specialized tactile responses to smoke, aiding in their ability to locate and lay eggs in burnt trees (Mitchell and Martin 1980). There is an obvious link between fire management practices and the potential impacts on the native arthropod community.

Restoration of Coastal Sage Scrub

Restoration is becoming a common tool for conserving habitat in S. CA. Unfortunately, restoration efforts are often very diverse, and lack any measures of success beyond simple plant survival. Little attention is given to restoring the ecosystem services and functions beyond what is observed in the plant community. Longcore (1999) conducted the most comprehensive study on the use of arthropods as indicators of CSS restoration success. Here, the use of arthropods as bioindicators was employed as an additional measure of the success for restored CSS. Overall arthropod diversity and evenness were significantly lower at restored sites than undisturbed control sites, even though the vegetation was similar. Non-native species of arthropods (Argentine ants, European Earwigs, and Sowbugs) were more commonly associated with restored sites. Longcore (1999) concluded arthropods are important indicators of restoration success, and should be included future monitoring efforts.

Other studies have shown physical disturbance to the landscape can produce declines in family richness (Kimberling et al. 2001). Both studies indicate we should expect both different responses from specific species/groups of arthropods to disturbance and potential complex ramifications through the CSS food web (Longcore 1999, Kimberling and Karr 2001). Therefore, we should be able to detect a response to disturbance by the invertebrate community, and use it in the development of an IBI.

Habitat Fragmentation

The effects of habitat fragmentation on the overall arthropod diversity and abundance have been observed in the CSS community (Suarez 1998, Bolger

2000). Arthropod diversity and abundance were positively correlated to fragment size, and negatively to time since isolation; spider diversity and abundance were enhanced by fragmentation, exotic ants reduced the richness and abundance of other arthropods; spiders and carabid beetles increased in abundance in older fragments, being positively correlated with the abundance of Argentine ants and exotic Isopods, Dermaptera, and Blattaria (Bolger et al. 2000).

Conclusion

The characteristics of arthropods make them ideal candidates for inclusion in an IBI. Within CSS, studies have found quantifiable responses to fire, mechanical disturbance and habitat fragmentation. Likewise, our ability to rapidly and efficiently assess the arthropod community in CSS provides a cost effective tool for evaluation. A host of other studies in different systems indicates substantial support for the use of arthropods in assessing ecological risk. Thus, we feel the arthropods will make up a key component of a terrestrial IBI for CSS.

Data gaps and recommendations for future research

Given the sparseness of studies and the complexity of the taxa, there are numerous directions for future research in S.CA arthropods. Significant data gaps exist in the overall distribution of many of the key taxa. The natural history of these organisms is also not well understood. We should also focus future efforts on the effects of fire on the arthropod community, how diverse interactions result in food web dynamics, the effects of pesticide use and exotic introductions on native taxa, and the role insect pollinators play in the CSS plant community. Regardless of the project’s focus, all future research should incorporate measurement of the abiotic factors at study sites. Many of the previously mentioned studies show the arthropod community assemblage is significantly influenced by the local abiotic conditions. We therefore recommend a minimal amount of abiotic data be gathered in addition to an biological data (e.g. temperature, relative humidity, and precipitation); along with a characterization of the site (e.g. elevation, distance from coast, vegetation type, soil type, etc.).

Table 6. Threatened or endangered species listed in California.

Status (Threatened = T; Endangered = E)	**Common Name**	**Scientific Name**
T	Beetle, delta green ground	*Elaphrus viridis*
E	Beetle, Mount Hermon June	*Polyphylla barbata*
T	Beetle, valley elderberry longhorn	*Desmocerus californicus dimorphus*
T	Butterfly, bay checkerspot	*Euphydryas editha bayensis*
E	Butterfly, Behren's silverspot	*Speyeria zerene behrensii*
E	Butterfly, callippe silverspot	*Speyeria callippe callippe*
E	Butterfly, El Segundo blue	*Euphilotes battoides allyni*
E	Butterfly, Lange's metalmark	*Apodemia mormo langei*
E	Butterfly, lotis blue	*Lycaeides argyrognomon lotis*
E	Butterfly, mission blue	*Icaricia icarioides missionensis*
E	Butterfly, Myrtle's silverspot	*Speyeria zerene myrtleae*
T	Butterfly, Oregon silverspot	*Speyeria zerene hippolyta*
E	Butterfly, Palos Verdes blue	*Glaucopsyche lygdamus palosverdesensis*
E	Butterfly, Quino checkerspot	*Euphydryas editha quino*
E	Butterfly, San Bruno elfin	*Callophrys mossii bayensis*
E	Butterfly, Smith's blue	*Euphilotes enoptes smithi*
E	Fly, Delhi Sands flower-loving	*Rhaphiomidas terminatus abdominalis*
E	Grasshopper, Zayante band-winged	*Trimerotropis infantilis*
T	Moth, Kern primrose sphinx	*Euproserpinus euterpe*
E	Skipper, Laguna Mountains	*Pyrgus ruralis lagunae*
E	Tiger beetle, Ohlone	*Cicindela ohlone*

Conclusions

The final task of this deliverable was to make recommendations regarding further research necessary to understand how CSS responds to disturbance. We have largely covered specific gaps in knowledge within the individual taxa reviews. We conclude with three main points.

1) Focused studies on taxa responses to disturbance are needed. Across all taxa, only a few studies were specifically designed to address CSS responses to disturbance. Furthermore, the majority of studies cover specific forms of disturbance for specific taxa. For example, plant ecologists have largely focused on CSS vegetation response following fire or to decreased fire interval, while studies of other impacts, such as invasive species are rare. Studies of animals have focused primarily on responses to patch size and isolation. These animal studies have primarily focused on the relatively small, urban canyons within the city of San Diego. Unfortunately, many of the NCCP reserves exist in much larger areas of land, making it difficult to extrapolate the findings of these smaller scale studies to the larger reserves. In conclusion, there are massive gaps in our knowledge of how many species, functional groups, and taxa, within CSS respond to disturbance.

Two general approaches could be used to begin filling in these data gaps. First, monitoring plans required by the NCCP should be designed to sample CSS taxa across gradients in various forms of disturbance. By randomly placing monitoring sites, or by focusing on “good” patches of CSS, reserve managers are missing an opportunity to gain critical information regarding responses to disturbance. By using “natural” variation in the level of disturbance, USFWS and CDFG managers can begin to infer how taxa respond to anthropogenic impacts. Experimental designs may include monitoring at various distances from edges, or across different types of edges (i.e. urban vs, agriculture); sampling in sites with different fire histories ranging from high to low fire average fire return intervals.

The second approach is to experimentally manipulate existing stands of CSS. Small amounts of CSS could be “sacrificed” to understand how particular disturbance regimes impact (or not) various CSS species or taxa. The degree of impact to CSS could be substantial if studies such as mechanical disturbance are implemented. We recommend experiments with less direct impacts, designed to study potentially subtle responses. For example, placing artificial lighting in an area to simulate light pollution would likely have little long-term impacts on a site, but could indicate those particular species highly sensitive to changes in light regimes.

2) Single species approaches to understand community-level responses are not well supported. Our review indicates the use of indicator species in CSS has not been successful and given the wide array of ecological specialization and response to disturbance already seen by species in CSS, we are doubtful of any future successes. Unfortunately, studies attempting to show relationships between single species and higher order metrics, such as overall species richness, have generally failed to find relationships.

Furthermore, our review indicates the remaining CSS is likely facing sustained levels of a variety of anthropogenic and biological (invasive species) impacts. As such, we feel relatively high levels of focused, active management will likely be required to sustain current levels of biodiversity in CSS. As such, we are not convinced an indicator species approach is useful for directing the types of management we envision as critical. For example, suppose an indicator species is discovered in the next two years. What should a manager do if the species is absent, or disappears at specific locations in their reserve? Without a more complete understanding of CSS responses to disturbance and the effectiveness of potential management practices, at this point in time, a reserve manager would be hard pressed to invoke new policies. We emphasize the need to first understand the ecological responses, which we currently do not yet know, then focus on finding efficient forms of monitoring.

3) A prioritization of possible management actions and simultaneous studies regarding their utility and cost-effectiveness is critical. As indicated in #2, our review convinces us active management will more likely be the rule than self-sustaining, easily managed systems. Furthermore, the number of economically, and logistically possible management actions possible at a site is relatively short. Broad categories in a list would likely include: altering fire regimes, minimizing human intrusion, restoring habitat, and controlling invasive species. As in #1 above, we need studies showing how effective different forms of these four broad management actions may be. In most cases, well-designed experiments will provide the greatest amount of information for the least cost. A current example is the CSS restoration study occurring on Metropolitan Water District at the Shipley reserve. This experiment is simultaneously testing the effectiveness of burning, grazing, and water addition on invasive grass control and CSS restoration. In addition to specific experiments, monitoring programs should be integrated into investigations of potential management actions by placing monitoring sites within manipulated and un-manipulated management units. To begin the process of selecting and studying the utility of management actions, we recommend a symposium focused specifically on 1) developing a “laundry list” of possible management actions and 2) synthesizing the current state of knowledge regarding which strategies work.

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