

A final report to project 369 – Red Rocks to the Summit – an assessment of spring and spring brook biodiversity values and the role of disturbance in shaping environmental conditions.

Introduction

Described in our proposal for the project research, which was drawn up in 2002, the Red Rocks to the Summit studies intended to assess the roles of various sources of disturbance as they affect biotic diversity at springs and associated spring brooks, and their wetland and riparian ecological communities in the Spring Mountains. The focal disturbance of concern was that caused by feral horses, and other ungulate grazers and browsers. Primary tools in assessing disturbance were to be before and after measurements of vegetation conditions, and plant and animal species richness at springs where exclosure fencing was to be installed or removed (experimentally and temporarily). Changes in the conditions of various elements of biodiversity would be measured across the period of management actions, then beyond. Because of changes in previously promised management actions by federal land managers, the pre-action/post action data collection scheme had to be altered; and was replaced with an intensive assessment of multiple plant and animal taxa in an experimental design that considers past and current disturbance stressors, including feral grazers.

The project mined historical data from the mountain range in reports submitted to, but not previously used by, the land management agencies. The project concurrently employed a multi-disciplinary team, which sampled vegetation (including plant species composition, structure, and other variables), aquatic invertebrates, butterflies, and measured disturbances at 32 springs and spring-courses (or subsets of them). The resulting data were analyzed for patterns and deterministic relations among physical characteristics of springs, their biotic attributes, and anthropogenically generated disturbances. The detail of the sampling have been described in quarterly reports, research reports, and in the methods sections of the attached published and in-draft technical papers. Results pertinent to the prioritization of spring resources began to emerge in early 2005, spawning multiple meetings with USFS resource staff (as well as BLM and FWS) that continue to present, which are designed to translate field findings into management friendly guidance from which targeted conservation actions and priority analysis has been carried out.

Many of the management-informing findings from this study are in a series of five published and in-progress scientific journal articles, which are appended to this report. More are in production. As described below these and other findings that are pertinent to current and future management actions and policy decisions have been vetted with the Forest Service and BLM in what have been described as adaptive management meetings, wherein resource management staff and our research team iteratively discussed our findings and ongoing and planned management activities, evaluations and re-evaluations of management actions were initiated. The research team continues to exchange with agency staff; the agencies sent our team an extensive series of management questions that are being treated in written response, which we will copy to Clark County.

Did this project achieve the indices of success contained in the project quarterly reports? What measurable goals did you set for this project and what indicators did you use to measure your performance? To what extent has your project achieved these goals and levels of performance?

The measurable goals met included multiple quarterly reports updating actions and project advances, a presentation on request to the IMC in September 2005, subcontracted work to identified scientists, meetings with appropriate agency staff, analysis and promulgation of data gathered and interpreted, and various status reports.

The expected delivered products include publication-worthy scientific data and analyses (adjusted for the amended approach taken when management actions by the land managers did not move forward), which have been forwarded as electronic data to the county, been analyzed and interpreted for scientific peer review, and have been interpreted in the context of real time management decisions and transferred to agency resources staff.

We believe we have met both explicit and implicit project goals during the contract period, and intend to extend data analysis and interpretation, as well as the dialogue with agency managers.

Did the project encounter internal or external challenges? How were they addressed? Was there something Clark County could have done to assist you?

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Just preceding and concurrent with initiation of project data collection a “gather” of feral horses was carried out in the mountain range, reducing by about half resident horse bands and individuals, and freeing many proposed study areas of horse generated impacts. The remaining horses were concentrated in a small portion of the range, including areas where

many remaining horses are provide food and water; the redistribution of horses and associated disturbances made obsolete the original range-wide data collection design, although not the need to understand the horse-ecosystem relationship.

Also affecting our experimental approach was an unanticipated change in the previously stated intention of the Forest Service to continue and expand on fencing efforts intended to enclose unprotected spring resources in efforts arrest impacts wetland vegetation from grazing. Instead of the planned construction of six to ten new exclosures each year from 2002 to the present, preceding this year (2005) just two fences were constructed. Clearly the proposed data collection prior to and following fencing actions was rendered not doable when the fencing plans did not move forward.

The implications of the two management adjustments on our proposed data collection activities and resource assessment efforts were straightforward. Given that the resource management and conservation challenge remained, but the study opportunities then differed greatly, we were forced to amend our proposed experimental design and approach. To meet the goals of our original proposal using an alternative approach, we could measure conditions (environmental responses of select biotic indicator taxa) at multiple sites across the range, which are or have been subject to different disturbance regimes. Using historical data as baselines (and analyzing those data for the first time), we selected a subset of springs in the mountain range (representing multiple gradients of management concern), and subjected them to intensive sampling for taxonomic groups selected to offer broad inference useful to management planning. The combined data sets gathered in field seasons 2003, 2004, and 2005 on wetland and riparian plants, adjacent upland plants, aquatic invertebrates, and butterflies constitute the most extensive biodiversity data sets from the Spring Mountains. We also assessed all signs of visitation and associated disturbances at each spring for which we have plant and animal data.

We are not sure that Clark County could have helped to facilitate easier transitions in data collection efforts under the changed management circumstances that the project encountered. However, one important change would be helpful to any other efforts that will follow this one on U.S. Forest Service lands in the Spring Mountains. Although the results of these and similar studies have direct application to specific land and resource management decisions and the prioritization of actions by the agency resource managers, it is not the USFS resource managers that interact with the county's HCP, but the (recreation) planning team. The planners (particularly administrators), frankly, have expressed hostility to the precepts of the HCP, impatience with having to consider species concerns in their long-range planning, and have proven to be utterly uncooperative and/or incompetent in their interactions with us (and others) in the context of adaptive management discussions. Only after we were "allowed" to communicate with the Forest Service resource staff did our research findings then generate the anticipated adaptive management dialogue (continuing to this date). Since working with agency resource management staff we have generated the dialogue described below, which has contributed to informing (not fully directed) 2005, 2006, and next year's allocation of resource management funds in issues related to springs and riparian restoration and conservation.

What lessons did you learn from undertaking this project?

This response category appears to be designed to allow management projects to convey experiences gleaned from practice that would not otherwise be articulated. We have attached manuscripts that describe taxa-specific distribution and abundance relationships with springs and associated stream courses. We have harvested a number of findings pertinent to management, future monitoring efforts, and integrated conservation planning. Key findings include:

Predictive relations weak, with physical parameters poorly correlated with biotic variables

High degree of uniqueness among springs in species composition

Weak or no correlative relationships among taxonomic groups

Disturbance and species richness not related

Non-native species richness elevated at intermediate levels of disturbance

Seasonal nature of invertebrate availability constrains temporal sampling opportunities

Surprising tendency for upland plants to “invade” the riparian zone

Volant species show at least some isolation with distance

Suggested applications include recognition that springs cannot be readily ranked in conservation context based on single or several physical or biotic variables, unique resource attributes at springs and in associated wetlands occur in both species-rich and comparatively species-poor spring systems (hence resource goals are not reached by protection or rehabilitation of a small set of sites), contemporary disturbance regimes appear not to have led to systematic losses of species, and the very most highly disturbed spring systems might be down graded to a description of ‘not recoverable without complete restoration,’ but others in moderately disturbed to near-pristine condition can benefit from management and would continue to support significant biotic resources. In concert these findings and others indicate that conservation opportunities in Spring Mountains springs are many, and that a hierarchy of management response to create implementation opportunities can continue to be employed in management planning dialogues between managers and researchers.

Data collection extended into autumn 2005, with several additional field exercises in early 2006. Accordingly some data analysis continues, and results will emerge throughout 2006. The above and other observations will be joined with conclusions that will emerge from continuing analyses of the extensive data set accrued during the past 24

months, and applied in the ongoing adaptive management dialogue that has been attended by USFS (resources staff), USFWS, and BLM.

Again please refer to appended manuscripts.

What impact do you think the project has had to date?

As discussed above, and as described in the proposal, an ongoing adaptive and resource management dialogue has been carried out with agencies in coordination with USFS resource management staff. A response document to a series of information queries submitted to the research team in the closing days of this effort is in construction and will be forwarded to the county.

Is there additional research or efforts that would complement or add to your project that could be conducted?

There still would remain value in carrying forth the manipulation and disturbance experiments that we originally proposed, but were obviated when management plans and follow through at the Forest Service changed. Current findings suggest many management guidance considerations that can go far to assist the agencies in prioritizing future actions, selecting sites for focal efforts, and setting an appropriate timetable for conservation action. Less clear are the necessary mechanical responses, including the site-specific actions that could ameliorate very specific impacts from the constellation of stressors that differentially impact each spring.

MANUSCRIPT #1

Effects of environmental heterogeneity and disturbance on the native and non-native
flora of desert springs

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ABSTRACT

Vegetation often is used as a decision variable for conservation and resource management. Because time and money are limited, it is useful to identify predictable relationships between measures of vegetation diversity or status, the physical environment, and disturbance; native and non-native plants may have different functional responses. Working toward development of effective, practical strategies for management and ecological restoration in the Spring Mountains, an isolated mountain range in the eastern Mojave Desert (Nevada, USA) that is a focus of regional conservation planning, we examined whether native and non-native assemblages of spring-associated plants have predictable relationships with elevation, springbrook length, and various land uses. We also tested whether alternative environmental criteria were associated with the degree of predictability of local species presences and absences. Consistent with work in other systems, species richness and cover of native plants tended to decrease as intensity of disturbance increased, whereas species richness (but not cover) of non-native plants tended to peak with intermediate disturbance. Our results may suggest that invasions of non-native plants at springs in the Spring Mountains are relatively recent, and that rapid restoration and management actions may help protect ecological processes and viability of native plants. Ability to predict the order in which individual species are likely to be extirpated from or colonize springs was limited, perhaps reflecting considerable environmental heterogeneity among springs.

KEY WORDS

biodiversity; conservation; disturbance; intermediate disturbance; invasive species;
management; nestedness; restoration; springs; Spring Mountains

INTRODUCTION

Characterizations of vegetation type and condition frequently serve as a cornerstone for conservation and land-use planning and management. Prevalent assessment methods such as Gap Analysis (Scott et al. 1993), which identifies gaps in representation of biological diversity in areas managed primarily for the long-term maintenance of native species and ecosystems, commonly use vegetation as basis for estimating the distribution of biodiversity (Noss 1987; Hunter 1988; Noss and Cooperrider 1994; Noon and Dale 2002). By evaluating vegetation structure and floristic composition, for example, land managers often can gauge whether a given area is likely to provide necessary and sufficient resources for wildlife species of concern (Mayer and Laudenslayer 1988; Boyce and McDonald 1999; Carroll et al. 2001). Information about the extent and condition of vegetation regularly is used to assess ecological responses to an array of natural and anthropogenic environmental changes (Nichols 1999; Rooney and Rogers 2002).

Financial and logistical obstacles make it impossible to conduct detailed floral inventories and monitoring across landscapes. Consequently, identification of predictable relationships between measures of vegetation diversity or status, and measures of the types and intensities of disturbance, has considerable management relevance. Examination of correlations between vegetation communities and the physical environment—i.e., description of fundamental ecosystem linkages—often must precede tests of potential correlations between vegetation and human influences.

In January 2001, the U.S. Fish and Wildlife Service (USFWS) issued a 30-year Multiple Species Habitat Conservation Plan (MSHCP) to Clark County, Nevada, to help

minimize environmental impacts from rapid expansion of the Las Vegas metropolitan area. Among the requirements of the MSHCP is development of a Conservation Management Plan for springs and spring-fed riparian area in the permit area. Some 20 of the 79 species for which incidental take (i.e., take resulting from otherwise lawful activities) is authorized by the MSHCP depend primarily on springs or spring-associated vegetation. Reliance of a substantial proportion of flora and fauna on springs and spring-fed aquatic systems is apparent in Clark County—typical of circumstances across the arid western United States (Gubanich and Panik 1986; Myers and Resh 1999).

The Spring Mountains, an isolated mountain range in the eastern Mojave Desert that covers approximately 4000 km² and contains approximately 300 springs, has become a principal focus of planning efforts under the Clark County MSHCP. Most of the Spring Mountains is under jurisdiction of the U.S. Forest Service and U.S. Bureau of Land Management; therefore, local information needs include assessments of relationships between vegetation, abiotic gradients, and human activities, which can be used to assist in prioritizing springs for multiple uses. Human activities that alter the structure and composition of vegetation include diversions of water for domestic and municipal use, livestock grazing, and recreation (Shepard 1993). Grazing and trampling by feral horses and burros also modifies the morphology and vegetation of springs. Accordingly, rates of extinction are higher for native species that occur at springs and spring-fed aquatic systems than for species associated with any other landscape feature in the region (Sada and Vinyard 2002).

Intentional and inadvertent introductions of non-native plants to springs, often in combination with agricultural activities and urbanization, constitutes another potential

stressor to ecological processes and cause of declines in the distributions of native taxa in the Spring Mountains (as elsewhere; see Higgins et al. 1999; Mooney and Hobbs 2000; Rejmanek 2000, Palumbi 2001). Invasion of non-native species in mesic environments tends to be accelerated by water diversion and other anthropogenic changes in flow regimes (Minckley and Meffe 1987, Eby et al. 2003). Thus, native and non-native species may have distinct responses to disturbance. Replacement of dominant native plants by invasive non-native plants can have cascading effects on occurrence and fecundity of birds and other faunal groups (Fleishman et al. 2003; Rood et al. 2003) and on coevolved interactions among species (Futuyma and Slatkin 1983; Mills et al. 1993; Kinzig et al. 2001; Soulé et al. 2003).

When springs are either desiccated or degraded severely, associated native plants and animals may be extirpated (Minckley and Deacon 1968; Johnson and Hubbs 1989; Sada and Vinyard 2002). The response of native and non-native spring biota to less acute levels of disturbance, however, is poorly understood. Few standardized biological surveys of springs and spring-fed riparian systems have been conducted, and most of those concentrated on springs that were minimally affected by disturbance (Resh 1983; Williams and Danks 1991; Anderson and Anderson 1995).

Working toward development of effective, practical strategies for management and ecological restoration (Sax et al. 2002; Lytle and Poff 2004), we examined whether native and non-native assemblages of plants at springs in the Spring Mountains have predictable relationships with the physical environment and land uses. First, we investigated whether species richness could be explained as a function of spring elevation or springbrook length. In general, species richness is expected to increase as elevation

and springbrook length increase. Elevation tends to be correlated with water temperature and chemistry (temperature and mineral content decrease as elevation increases), whereas springbrook length is positively correlated with discharge. Second, we tested whether species richness and cover of different functional groups varied as a function of the intensity of natural and human disturbance. Third, we tested whether alternative environmental criteria were associated with the degree of predictability of local species presences and absences.

METHODS

Study system

The Spring Mountains extend in length nearly 125 km and span an elevational gradient from 1500 m at their base in Las Vegas Valley to 3632 m on Charleston Peak. As elevation increases, annual precipitation increases from less than three cm to more than 55 cm. Summer temperatures may reach 46° C at the lower end of the elevational gradient, decreasing to -9° C at relatively high elevations during the winter (Hidy and Klieforth 1990).

Most of the springs in the Spring Mountains are small and isolated, and many have been excavated or otherwise developed. Diversion structures, such as spring boxes to collect water and pipes to transport water to nearby troughs or tanks, are common. Numerous non-native species (primarily plants) have colonized these springs, and many springs are impacted by stochastic environmental phenomena, such as fire, avalanche, and flood. Nonetheless, some springs appear to have been minimally affected by either natural or anthropogenic disturbance. Among springs, there is considerable variation in

size; microclimate, topography, and soils; disturbance history; and other characteristic attributes.

Field methods

During July 1995, 50 springs were sampled that collectively span abiotic and disturbance gradients in the Spring Mountains. An additional 13 springs were sampled during summer 1997. Timing of sampling was intended to maximize our ability to identify and characterize spring-associated vegetation. Surveys focused on spring sources and their springbrooks immediately downstream. The entire area of each spring was sampled when the length of the springbrook was less than 50 m. At more extensive springs, surveys were constrained to upstream reaches with a distinctive riparian assemblage and sampling effort was approximately equal per unit area. Physical characteristics were recorded at the spring source and for approximately 50 m downstream.

Plants were identified to species whenever possible; in some cases, plants only could be identified to genus. Each taxon was categorized as native or non-native to the Spring Mountains. Whenever possible, plants also were categorized with respect to moisture requirements using data from Reed (1988) supplemented with the knowledge of experienced local ecologists. Wetland taxa are those that almost always or usually occur in wetlands with permanent water, upland taxa almost always or usually occur in non-wetlands, and facultative taxa are equally likely to occur in wetlands or non-wetlands.

The percent cover of each plant taxon was estimated visually in the sampled area using twelve cover classes: < 1%, 1 – 4.9%, 5 – 14.9%, 15 – 24.9%, 25 – 34.9%, 35 –

44.9%, 45 – 54.9%, 55 – 64.9%, 65 – 74.9%, 75 – 84.9%, 85 – 94.9%, > 95%. Midpoints of the cover classes were used for statistical analyses. We calculated cover of native and non-native plants at each spring by summing cover values for all taxa in either category. Because midpoints were used, those values may sum to > 100%.

Each spring was categorized as undisturbed, slightly disturbed, moderately disturbed, or highly disturbed. We categorized springs with respect to composite or total disturbance (i.e., no discrimination between the highest level of disturbance by either natural or anthropogenic sources), and also with respect to intensity of grazing, recreation, and water diversion. Grazing reflected use by any combination of cattle, elk, and feral horses and burros. Undisturbed springs appeared to be unaffected by historical or recent human land use, and slightly disturbed springs had little evidence of vegetation or soil disturbance. It was impossible to determine whether springs in these two categories never had been disturbed, or whether they had reached an alternative stable state following historical disturbances. Disturbances that appeared to have occurred within recent months or years were evident at moderately disturbed and highly disturbed springs. We categorized springs with vegetation covering > 50% of their banks and at least 50% of natural discharge remaining in diverted spring brooks as moderately disturbed. Springs with vegetation covering < 50% of their banks, that contained < 50% of natural discharge, or were either impounded, dredged, or recently disturbed by natural events were categorized as highly disturbed. Ephemeral springs were categorized as highly disturbed because of their reduction in flow.

Analyses

We used simple linear regression to test whether species richness of plants could be explained as a function of spring elevation or springbrook length. We used analysis of variance to test whether species richness and cover varied as a function of intensity of the four types of disturbance (composite or total disturbance, grazing, recreation, and water diversion). When there was a significant effect of a given type of disturbance, we used least-squared differences to compare intensity categories. Analyses of species richness, which included data from both 1995 and 1997, were restricted to perennial taxa that are less likely than annual taxa to fluctuate in occurrence between years.

To test whether assemblage structure was predictable with respect to alternative environmental criteria and functional groupings of species, we used nestedness analyses. Nestedness analyses are a relatively fast, straightforward tool for identifying environmental gradients that may influence species richness and species composition in a set of terrestrial or aquatic “islands” across both space and time (Wright et al. 1998). A nested biota is one in which the species present in relatively depauperate locations are subsets of the species present in locations that are richer in species (Patterson and Atmar 1986). Nestedness is a property of assemblages or communities, not of individual species (Wright et al. 1998), and has been interpreted as a measure of biogeographic order in the distribution of species (Atmar and Patterson 1993).

Nestedness analyses are effective tools for conservation and land-use planning because they can suggest, albeit via correlation, whether virtually any environmental variable of interest is likely to affect species richness and species composition in an array of locations (e.g., Kadmon 1995; Fleishman and Mac Nally 2002). Moreover, the comparative nestedness of different subsets of an assemblage may reflect species-specific

probabilities of extinction and colonization with respect to a given source of environmental change. Separately testing whether different functional groups (or native species and non-native species) are nested can provide useful information for management (Donnelly and Marzluff 2004). Differential nestedness among functional groups that vary in sensitivity to the availability of a particular resource, for example, suggests that the land uses or other processes affecting the provision of that resource are driving local extinction or colonization events (Hecnar and M'Closkey 1997; Fleishman and Murphy 1999; Jonsson and Jonsell 1999). By providing information on distributional patterns and suggesting potential underlying mechanisms, nestedness analyses can inform efforts to prioritize locations for conservation, human activities, or investments in ecological restoration (Margules and Pressey 2000). Even low degrees of nestedness can be informative, indicating that assemblage structure may be strongly affected by stochastic processes, therefore may be difficult to manipulate by changes in land management.

Presence / absence matrices for nestedness analysis typically are assembled by arranging locations or sites as rows in order of decreasing (top to bottom) species richness, and species as columns in order of decreasing (left to right) prevalence. This ordering provides a description of assemblage structure and is the first step in a more-detailed examination of nestedness. If one wishes to test whether a particular environmental variable may be related to a nested distributional pattern, then rows may be ordered with respect to that criterion instead of by species richness (Fleishman and Mac Nally 2002). For example, listing rows in order of decreasing area quantifies the degree to which biotas are nested by area. If an assemblage is nested with respect to a

selected environmental variable—or if an assemblage is more nested with respect to one environmental variable than another—it suggests that the variable in question has a non-trivial effect on species richness and species composition in the assemblage.

To test whether spring-associated plants were nested with respect to elevation and springbrook length, we computed the relative nestedness index C (Wright and Reeves 1992) with the program NESTCALC (Wright et al. 1990). We estimated statistical significance using Cochran's Q statistic (Wright and Reeves 1992). Values of C vary between 0 and 1.0, approaching 1.0 for perfectly nested matrices. A key advantage of this metric is that it allows for statistical comparison of degree of nestedness among matrices or data sets. Moreover, C is not highly sensitive to matrix size (Wright and Reeves 1992; Bird and Boecklen 1998). We used Z scores (standard-Normal variates) to test whether significant differences existed in relative nestedness among matrices ranked by different environmental criteria (Wright and Reeves 1992). We also tested whether degree of nestedness was significantly different between springs in different composite disturbance categories and whether degree of nestedness was significantly different between native and non-native plants.

RESULTS

Species richness of perennial plant taxa at our 63 study springs ranged from three to 30 (mean 14.0 ± 5.5 SD). We recorded a total of 215 perennial taxa; individual taxa were present at one to 24 springs. Most taxa had low occurrence rates. Only 49 taxa (0.23) were present at five or more springs, and 88 taxa (0.41) were present at just one spring. A high proportion of the taxa recorded (0.89) are native to the Spring Mountains.

Sixty of the taxa we recorded at springs and in spring-fed riparian sites almost always or usually occur in wetlands (0.28), whereas 106 taxa (0.49) almost always or usually occur in non-wetland (or upland) land cover. Twenty-six taxa (0.12) are equally likely to occur in wetlands or non-wetlands. The mesic association of 23 taxa (0.11) could not be determined. Complete data are available from the corresponding author on request.

Thirteen springs were categorized as undisturbed. The number of springs categorized as slightly disturbed, moderately disturbed, and highly disturbed was 16, 13, and 21, respectively. Sampled springs covered an elevational gradient from 1082 to 3097 m. Springbrook length ranged from 0 to 5000 m.

Effect of elevation and springbrook length on species richness

Elevation did not have a statistically significant effect on species richness of plants (all species, native species, or non-native species). Richness of non-native species increased as springbrook length increased ($F_{1,62} = 4.05$, $P < 0.05$), but the proportion of variance in species richness explained by springbrook length was low ($R^2 = 0.05$).

Effect of disturbance intensity on species richness

Total species richness of plants varied as a function of overall disturbance intensity ($F_{3,59} = 6.60$, $P < 0.01$). Species richness was lower at highly disturbed springs than at springs in any other disturbance category. Species richness of native plants was lower at highly disturbed springs, and higher at undisturbed springs, than at slightly or moderately disturbed springs ($F_{3,59} = 8.57$, $P < 0.001$) (Figure 1). Species richness of

non-native plants also varied along the disturbance gradient, but with a different functional response ($F_{3,59} = 2.88$, $P < 0.05$) (Figure 1): species richness was lower at undisturbed springs than at slightly or moderately disturbed springs.

Disturbance intensity had a significant effect on species richness of wetland plants and plants that occur facultatively at wetlands. Species richness of wetland plants was lower at highly disturbed springs than at springs in any other disturbance category ($F_{3,59} = 4.58$, $P < 0.01$). Species richness of facultative plants was lower at highly disturbed springs than at either undisturbed or slightly disturbed springs ($F_{3,59} = 5.01$, $P < 0.01$). Disturbance did not have a statistically significant effect on species richness of upland plants.

Effect of type of disturbance on species richness

Species richness of all plants ($F_{3,59} = 5.13$, $P < 0.01$) and species richness of native plants ($F_{3,59} = 6.29$, $P < 0.001$) had the same functional response to intensity of grazing: species richness was lower at springs with high grazing intensity than at springs with either no grazing or slight grazing (Figure 2). Species richness of non-native plants, by contrast, was greater at springs with moderate grazing intensity than at springs with either no grazing or high grazing intensity ($F_{3,59} = 2.92$, $P < 0.05$) (Figure 2).

Water diversion also affected species richness. Species richness of all plants ($F_{3,59} = 6.48$, $P < 0.001$) and species richness of native plants ($F_{3,59} = 8.06$, $P = 0.001$) was lower at springs with high diversion than at springs with no diversion or moderate diversion (Figure 3), whereas species richness of non-native plants was higher at springs with slight diversion than at springs with either no diversion or high diversion ($F_{3,59} = 2.71$, $P = 0.05$) (Figure 3). Intensity of recreation did not have a significant effect on species richness.

Effect of intensity and type of disturbance on plant cover

Cover of native species was lower at highly disturbed springs than at springs in any other disturbance category ($F_{3,46} = 8.71$, $P < 0.001$) (Figure 4). Cover of non-native species did not vary as a function of composite disturbance.

Water diversion was the only type of disturbance that had a significant effect on cover of native species. Cover of native species was lower at springs with high diversion than at springs with no diversion or slight diversion ($F_{3,46} = 7.62$, $P < 0.01$) (Figure 5). No type of disturbance had a significant effect on cover of non-native species.

Nestedness

The distributional pattern of plants was significantly nested regardless of whether matrix rows were ordered by species richness, elevation, or springbrook length, but values of the relative nestedness index C were low (Wright et al. 1998; Table 1). Thus, although the plant assemblages in relatively depauperate sites were statistically proper subsets of the species present in relatively species-rich locations, there was considerable “noise” in the overall nested pattern. Consequently, the potential of nestedness analyses to reliably predict the order of species extirpation or colonization in this system is limited. The subset of native plants had a significantly nested distribution, as did the subset of non-native plants (Table 1), but the difference in relative nestedness between native plants and non-native plants was not statistically significant. Plant assemblages at slightly disturbed and highly disturbed springs also had significantly nested distributions, but relative nestedness did not vary among disturbance categories (Table 1). On the whole, these results suggested that stochastic processes play an important role in assemblage structure of both native and non-native plants.

DISCUSSION

Two strong messages emerge from our analyses. First, native and non-native plants appear to have different functional responses to disturbance. Second, current distributions of individual species largely may reflect environmental heterogeneity rather than a predictable response to human land use.

Overall, native and non-native species exhibited different functional responses to disturbance (both composite disturbance and specific types of disturbance). Species

richness and cover of native plants tended to decrease as intensity of disturbance increased, whereas species richness of non-native plants tended to peak with intermediate disturbance. These results are consistent with other studies and reviews suggesting that species richness often has a predictable response to gradients of natural disturbance and human land use (McIntyre 2000; Blair 2001; Pickett et al. 2001). The functional form of the response usually depends in part on whether a particular disturbance augments or reduces resources for a given taxonomic group, whether species have adapted to that disturbance over evolutionary time, and whether species are affected by the presence of human activities per se. Along an urbanization gradient, for example, species richness often peaks in locations with an intermediate degree of urban development (Blair 1999). The latter pattern typically reflects an increase in the number of synanthropic species (native and cosmopolitan species that are associated with humans) or non-native species with general resource requirements that benefit from irrigation, fertilization or augmentation of food resources, and other inputs (Blair 1999; Donnelly and Marzluff 2004). Many native species, by contrast, are restricted to locations with relatively little urban development (McKinney 2002).

Grazing and water diversions, like urbanization, often favor the establishment of generalists and invasive non-native species over the persistence of native species. In wetlands, for instance, invasion of non-native species tends to be accelerated by anthropogenic changes in flow regimes (Minckley and Meffe 1987; Eby et al. 2003). Interestingly, we did not find a significant relationship between disturbance and cover of non-native species of plants. In our study system, mean cover of native species was significantly greater than mean cover of non-native species ($t_{[49]} = -9.89$, $P < 0.001$).

Therefore, our results may suggest that invasions of non-native plants are relatively recent and many of those species have not yet expanded their distributions among isolated wetlands. Limited colonization of non-natives also may be a function of environmental heterogeneity and the absence of resources for given non-native species at individual springs.

Although annual plant species were excluded from the majority of our analyses, examination of their patterns of occurrence may provide some useful information about emerging threats to ecological condition and associated management challenges. We recorded 34 annual plant taxa, 20 (0.59) of which were native. Thus, the ratio of native to non-native taxa was considerably lower for annuals than for perennials. As many as five native annuals (0.62 ± 1.01 , mean \pm SD) and seven non-native annuals (1.40 ± 1.48 , mean \pm SD) were present at a given spring. Non-native annuals tended to be more widespread than native annuals; non-natives were present at one to 17 springs each, whereas natives were present at one to five springs.

A high proportion of species were present at a small number of springs, and degree of nestedness was minimal. Values of the relative nestedness index C for our system were low relative to most values that have been reported for assemblages of different groups around the world (Cook and Quinn 1995; Boecklen 1997; Wright et al. 1998). For example, of the 148 matrices examined by Boecklen (1997), only 11 had values ≤ 0.100 . Weak nestedness may reflect underlying mechanisms including environmental heterogeneity, local endemism or adaptation, or differences in biogeographic history among species (Wright et al. 1998). In addition, there is a modest correlation between matrix fill and degree of nestedness—low C -values are characteristic

of systems in which a high proportion of species have low occurrence rates (Wright et al. 1998). In the Spring Mountains, lack of order in species composition of plants may be explained by variability in the abiotic and biotic attributes of springs as well as differences in colonization patterns between native and non-native plants. Populations of native species likely have been isolated in distinct local environments for prolonged periods of time, whereas the expansion of non-natives—in part facilitated by the movement of humans and livestock—has been comparatively recent and rapid. We emphasize that lack of nestedness does not mean assemblage composition is random or immune to ecological processes—it simply means that the order of species composition cannot be predicted according to a nested model (Worthen 1996).

An ability to predict how environmental changes will affect patterns of species richness and occurrence across a landscape increases the scientific information base for decision-making and development of conservation and land use plans. Apparently limited ability to forecast the order in which plant species are likely to disappear from or appear at springs in the Spring Mountains may simply reflect the tremendous variation in vegetated spring area, morphology, and disturbance history. Springs are influenced by regional and local geology, climate, and groundwater hydrology (Freeze and Cherry 1979; McCabe 1998). In the Spring Mountains, some springs dry each year, some dry only during extended droughts, and some persist presumably for millennia. This range of conditions is echoed by the diversity and high levels of endemism among aquatic and riparian plants and animals that inhabit springs (Resh 1983; Skinner 1994; Cushing 1996). Studies of aquatic macroinvertebrates in the Spring Mountains and other landscapes characterized by frequent, unpredictable disturbances have suggested that

individualistic, taxon-specific responses to environmental gradients are common in such systems (Heino et al. 2003; Sada et al. in press). Our work emphasizes, however, that life history of different functional groups affects their response to disturbance and, by extension, selection of strategies to maximize or minimize representation of the group across the landscape. The suggestion that non-native plants may not be long-established or well-established at springs in the Spring Mountains is just cause for optimism—rapid restoration and management actions may prevent these species from substantially modifying natural ecological processes and patterns of distribution and abundance of the range's native biodiversity.

ACKNOWLEDGMENTS

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FIGURE LEGENDS

Figure 1. Mean species richness of perennial plants as a function of intensity of disturbance. Bars with different letters are significantly different at $P \leq 0.05$.

Figure 2. Mean species richness of perennial plants as a function of intensity of grazing. Bars with different letters are significantly different at $P \leq 0.05$.

Figure 3. Mean species richness of perennial plants as a function of water diversion. Bars with different letters are significantly different at $P \leq 0.05$.

Figure 4. Mean cover of plants as a function of intensity of disturbance. Bars with different letters are significantly different at $P \leq 0.05$.

Figure 5. Mean cover of plants as a function of water diversion. Bars with different letters are significantly different at $P \leq 0.05$.

Table 1. Size and values of the relative nestedness index C for (a) matrices with rows ordered by different environmental criteria, (b) species with different residency status, or (c) matrices that included springs in different disturbance categories (ordered by species richness). Degrees of freedom are (number of species – 1). *, $P < 0.05$.

row order	springs	taxa	C
species richness	63	215	0.079*
elevation	63	215	0.061*
springbrook length	63	215	0.065*
status	springs	taxa	C
native	63	192	0.081*
non-native	23	43	0.044*
disturbance category	springs	taxa	C
undisturbed	13	117	0.017
slightly disturbed	16	124	0.037*
moderately disturbed	13	99	0.011
highly disturbed	21	111	0.026*

FIGURE 1

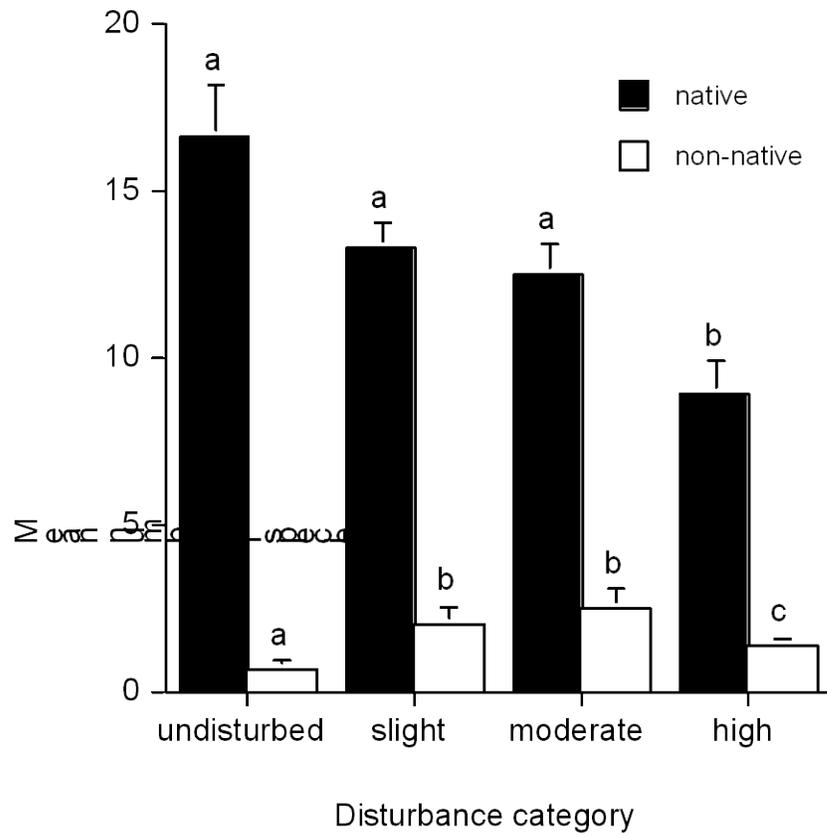


FIGURE 2

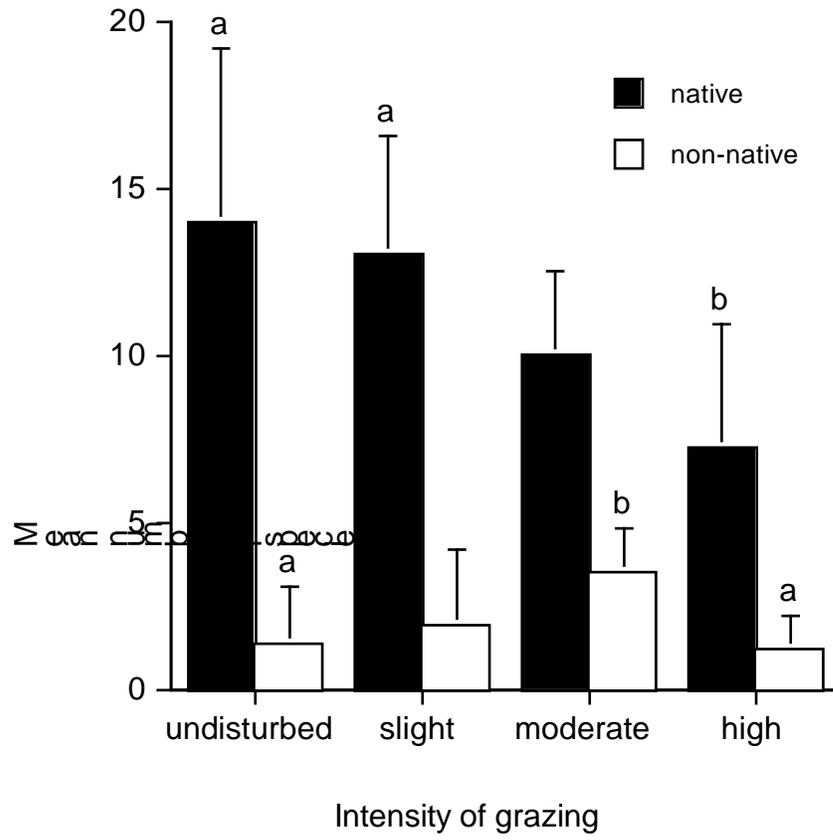


FIGURE 3

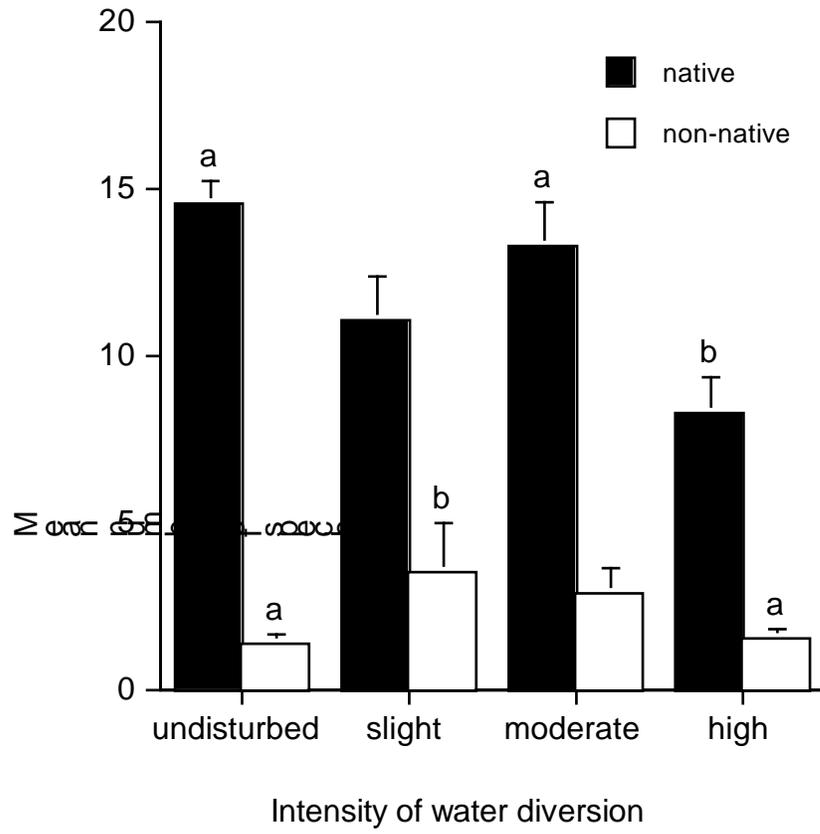


FIGURE 4

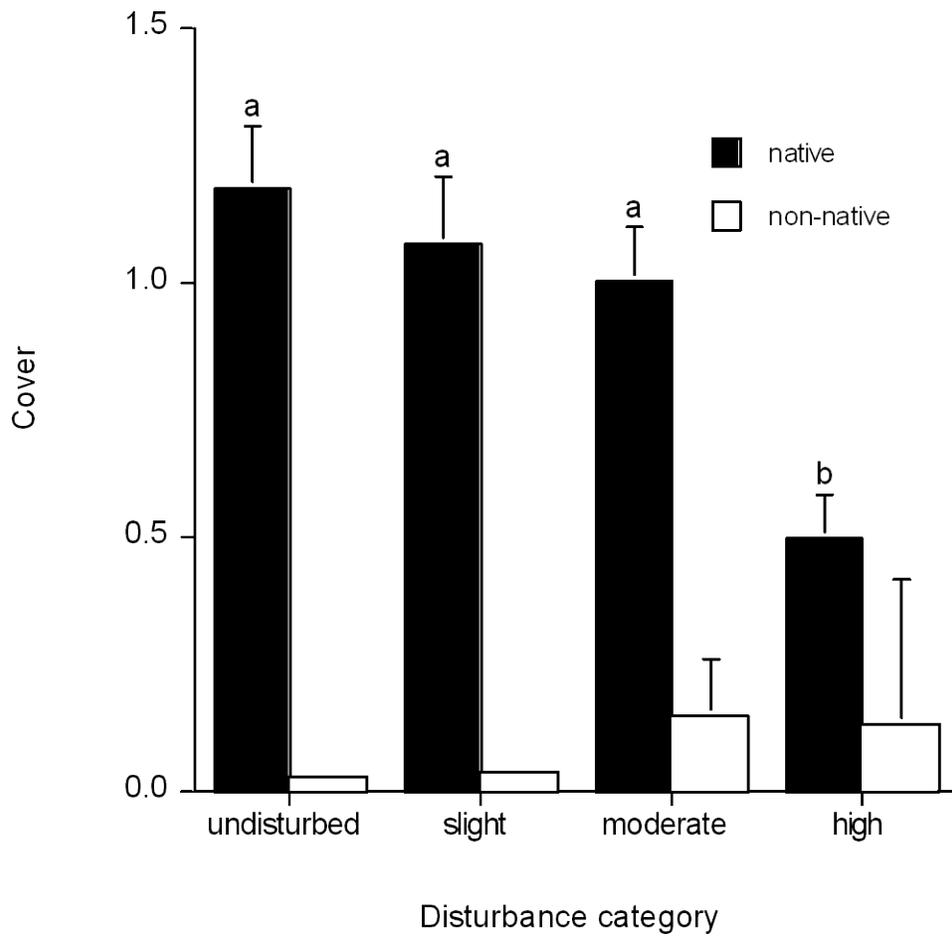
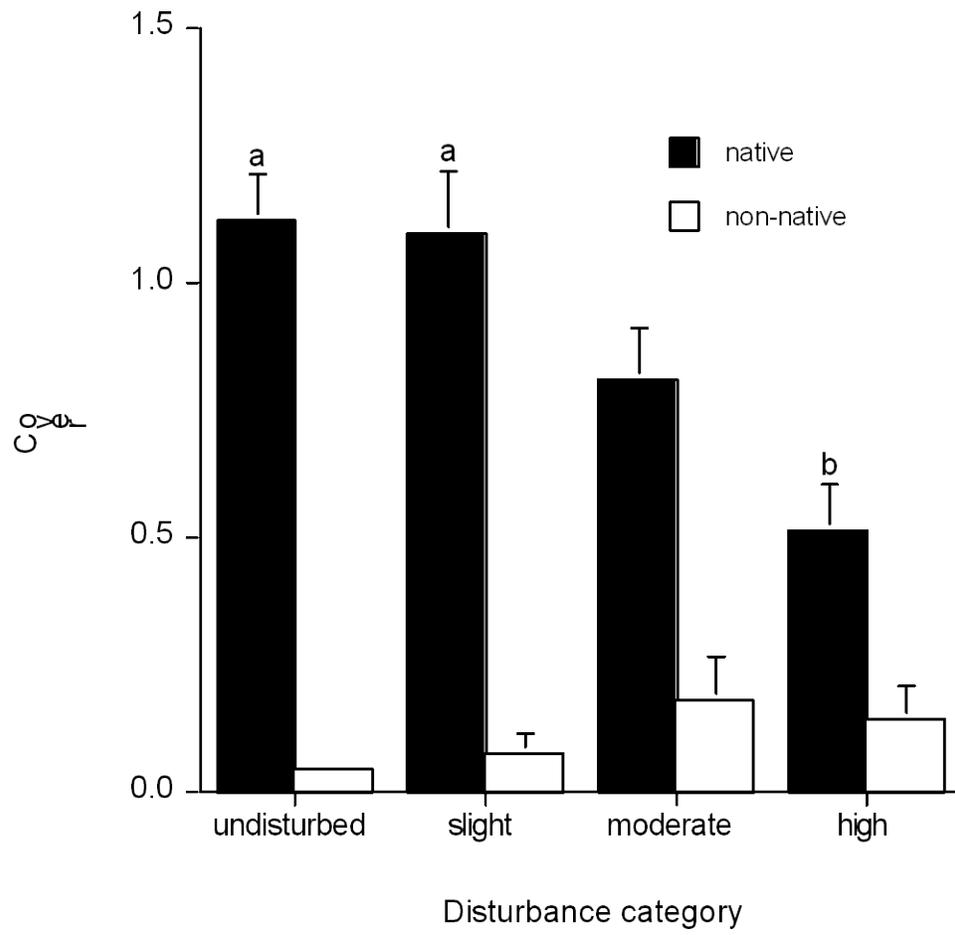


FIGURE 5



MANUSCRIPT #2

Biodiversity patterns of spring-associated butterflies in a Mojave Desert mountain range

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ABSTRACT. We examined whether species richness (number of species), abundance, and species composition (identity) of butterflies at 23 springs in the Spring Mountains, an isolated mountain range in the eastern Mojave Desert (Nevada, USA), had a predictable response to presence of riparian vegetation. The Spring Mountains are the focus of regional conservation planning, and managers are charged with prioritizing its springs for conservation and rehabilitation. We therefore used butterflies to help provide information on faunal responses to potential changes in land cover. Species richness and abundance of butterflies in locations with riparian vegetation consistently was higher than in locations with non-riparian vegetation across several levels of spatial resolution. Similarity of species composition of butterflies decreased as the linear distance between springs increased. Neither local presence of larval hostplants nor vegetation association (riparian or non-riparian) of larval hostplants had a significant effect on occurrence rate or abundance of individual species of butterflies. Nestedness analyses demonstrated that species present in locations with few species of butterflies tended to be subsets of the species present in locations that were richer in species, but that pattern did not appear to be driven by the availability of riparian habitat. The species that were present at the greatest number of springs tended to be geographically widespread taxa that can exploit human and natural disturbances. Our results suggest that reduction in water availability and the extent of riparian vegetation at montane springs in the Mojave Desert is likely to reduce local species richness and abundance of butterflies. The ability of broad categories of vegetation to serve as a predictor of species richness and composition of butterflies, however, may be relatively low.

ADDITIONAL KEY WORDS. conservation, isolation, nestedness, riparian, Spring Mountains

Springs and spring-fed aquatic systems support a substantial proportion of aquatic and riparian species in the arid western United States (Williams & Koenig 1980, Gubanich & Panik 1986, Myers & Resh 1999). Not only do several hundred endemic species and subspecies of aquatic vertebrates, invertebrates, and plants depend on springs, but springs provide resources for as many as 80% of terrestrial species (Hubbs & Miller 1948, Thomas et al. 1979, Hershler et al. 2002).

Because springs are the only reliable source of water across much of the western United States, human land uses also have tended to concentrate around springs. These uses include diversion of water for domestic and municipal use, livestock grazing, and recreation (Shepard 1993). Moreover, both intentionally and inadvertently, humans have introduced numerous non-native species of animals and plants to springs (Hendrickson & Minckley 1984, Sada & Vinyard 2002), leading to changes in biodiversity patterns and ecological processes (Mills et al. 1993, Kinzig et al. 2001, Soulé et al. 2003). Rates of extinction in the western United States currently are higher for native species that occur at springs and spring-fed aquatic systems than for species associated with any other category of landscape features (Sada & Vinyard 2002). As a result, restoration and rehabilitation of aquatic and riparian areas, often with a focus on vegetation communities, has become a top management priority.

Understanding how native faunal assemblages respond to availability of water and composition of vegetation in spring-fed riparian systems is critical to development of effective, practical strategies for ecological restoration and maintenance. The Clark County Multiple Species Habitat Conservation Plan (MSHCP), issued by the U.S. Fish and Wildlife Service in 2001, illustrates why this information has become so important. Thanks to explosive growth of the Las Vegas metropolitan area, Clark County is the most rapidly urbanizing municipality in the

United States. The MSHCP, which covers 79 species, is intended to mitigate the cumulative effects of urbanization while giving participants greater security about future regulatory restrictions. Among the requirements of the 30-year MSHCP is development of a Conservation Management Plan for springs in the permit area. The Spring Mountains, an isolated mountain range in the eastern Mojave Desert that covers about 4000 km², contains approximately 300 springs, and largely is public land, has become a principal focus of these planning efforts.

Few standardized biological surveys have been conducted at springs in the Spring Mountains. Among invertebrates, several well-known taxonomic groups, including tiger beetles and butterflies, are thought to be associated strongly with changes in land cover (Kremen et al. 1993, New et al. 1995, Carroll & Pearson 1998, Rodrigues et al. 1998). Because invertebrates have relatively short generation times, they may be useful for exploring how expansion or contraction of riparian cover affects native fauna. In this paper, we present the early results from an ongoing study that uses butterflies as a case-study group to infer how changes in water availability and land cover at springs may affect native fauna. As a first step, we have examined patterns of species richness and abundance of butterflies associated with broadly categorized riparian and non-riparian vegetation. We are in the process of collecting detailed data on vegetation composition and structure to increase understanding of potential mechanisms driving the patterns reported here and to help guide regional conservation and restoration efforts.

METHODS

Study system. The Spring Mountains are ca 125 km in length and span an elevational gradient from 1500 m in Las Vegas Valley to 3632 m on Charleston Peak. As elevation increases, annual precipitation increases from less than three cm to more than 55 cm. Summer

temperatures may reach 46° C at the lower end of the elevational gradient, decreasing to –9° C at relatively high elevations during the winter (Hidy & Klieforth 1990).

Most of the springs in the Spring Mountains are small and isolated, and many have been excavated or otherwise developed. Diversion structures, such as spring boxes to collect water and pipes to transport water to nearby troughs or tanks, are common. Numerous non-native species (mostly plants and fishes) have colonized these springs, and many springs are impacted by stochastic environmental phenomena such as fire, avalanche, and flood. Nonetheless, some springs appear to be in good condition and have been minimally affected by either natural or anthropogenic disturbance.

The butterfly fauna of the Spring Mountains is particularly well known and has been subject to intensive sampling for more than two decades (Austin & Austin 1980, Austin 1981).

Field Methods. Between April and August 2003, we conducted surveys of butterflies at 23 springs that collectively span major environmental and land-use gradients in the Spring Mountains. Visits were conducted once per month for a total of five visits per spring. Phenologies of butterflies and plants were similar among springs. Surveys were conducted when weather conditions were most conducive to flight (e.g., mostly sunny, light winds, warm temperatures). Although stronger inferences could be drawn if more than one year of data were available, the sample year 2003 experienced representative weather conditions, it was neither particularly dry nor particularly wet. Annual precipitation for 2003 at Red Rock Canyon State Park in the Spring Mountains was 24.2 cm; the mean for the 17-year period of record is 29.4 cm (± 13.6 SD) (Western Regional Climate Center 2004).

Sampling effort was roughly proportional to length of the springbrook (i.e., sampling effort was approximately equal per unit area). We established sampling points at the spring source; 30 m from the source at 0°, 90°, and 270°; and at 100 m intervals downstream from the source along the length of the springbrook. Vegetation at each sampling point was categorized as either riparian or largely non-riparian. Riparian taxa were defined as those that almost always or usually occur in wetlands with permanent water (Reed 1988). Examples of local riparian taxa include *Eleocharis*, *Equisetum*, *Juncus*, and *Muhlenbergia*. Although the existence of non-riparian vegetation at a spring may seem to be a contradiction in terms, many springs are ephemeral, with flow rates that fluctuate seasonally or annually. As a result, plants that do not depend on permanent sources of water (e.g., *Bromus*, *Penstemon*, *Poa*) often become established near the spring source and along the springbrook. As noted above, our vegetation categorizations were intentionally broad; categorizations will be refined and quantified following collection of additional data.

We established a circle with a 10 m radius at the center of each sampling point. During each visit to each spring, using methods that have proven effective in other riparian areas in the Mojave Desert and Great Basin (Fleishman et al. 1999, Mac Nally et al. 2004), an experienced observer identified and recorded all butterflies seen during a 10 min period within the circle. In preliminary “mock” surveys, more than 10 min in a sampling point almost never resulted in the detection of additional species of butterflies. Because sampling effort was approximately equal per unit area of the spring, the risk of sampling error was relatively uniform. Individual butterflies typically did not appear to be move among sampling points during each visit to each spring. We calculated species richness (number of species) and abundance (number of individuals) of butterflies over the five-month sampling period for each spring. Where applicable, we also calculated separately species richness and abundance of butterflies associated with riparian and non-riparian vegetation at each spring.

Larval hostplants have been identified for virtually all species of butterflies that inhabit the Spring Mountains (G. T. Austin pers. com.). For each species of butterfly that we recorded, we categorized the occurrence and vegetation association of its larval hostplant(s) across the suite of springs we surveyed as present, riparian; present, non-riparian; or absent.

Analyses. We used analysis of variance to test whether species richness and abundance of butterflies varied as a function of vegetation association (riparian versus non-riparian) across all springs. We also used paired *t*-tests to compare species richness and abundance of butterflies associated with riparian versus non-riparian vegetation at the 18 springs with both types of plant communities.

We calculated similarity (Canberra distances) of species composition (i.e., species identity) of butterflies among all springs, among the riparian component of springs, and among the non-riparian component of springs. We used Mantel tests (Mantel 1967, Douglas & Endler 1982) to evaluate whether similarity of species composition of butterflies decreased as linear distance between springs increased. Canberra distances and Mantel tests were calculated using the *R* Package (Casgrain & Legendre 2001).

We used analysis of variance to examine whether occurrence rate (i.e., the number of springs at which each species was present) or abundance of butterflies varied as a function of the occurrence or the vegetation association of their larval hostplants in the study system.

To test whether predictability of patterns of species richness and composition varied between riparian and non-riparian vegetation, we used nestedness analyses. Nestedness analyses have greatly expanded our capacity to understand biotic patterns across networks of terrestrial or aquatic islands of resources or habitat (Wright et al. 1998). Nestedness analyses test the degree to which species present in relatively species-poor locations are proper subsets of species present in relatively species-rich locations (Patterson & Atmar 1986, Wright et al. 1998). Nestedness is a property of assemblages, not of individual species, and has been interpreted as a measure of biogeographic order in the distribution of species (Atmar & Patterson 1993).

Numerous studies have demonstrated that nested distributional patterns are common across taxonomic groups and ecosystems. The accuracy of predictions of the sequence in which species will be extirpated from or colonize a set of locations occupied by a nested assemblage is positively correlated with the degree of nestedness. Assemblages can be nested by multiple phenomena, including but not limited to species-specific probabilities of extinction, species-

specific probabilities of colonization, and nestedness of resources or habitat types (Darlington 1957, Cook & Quinn 1995, Lomolino 1996).

Nestedness analyses are effective tools for management because they can suggest, albeit via correlation, whether virtually any environmental variable of interest is likely to affect distributional patterns in an array of locations (e.g., Kadmon 1995, Fleishman & Mac Nally 2002). Differential nestedness among groups of species (e.g., functional groups or guilds) that vary in sensitivity to the extent of a particular type of land cover, for example, suggests that the processes affecting the occurrence and extent of that land cover type are driving local extinctions or colonizations (Hecnar & M'Closkey 1997, Fleishman & Murphy 1999, Jonsson & Jonsell 1999). It may not always be possible to establish a causal relationship between environmental variables and species occurrence, but strong correlations can, at minimum, help refine process-based hypotheses that can be tested with more intensive experiments or observations. Nestedness analyses have realistic application because they provide information on patterns and suggest mechanisms affecting not only species richness but also species composition. These data can inform decisions about how to maximize richness of native species across a multiple-use landscape (Margules & Pressey 2000).

To test whether assemblages were nested with respect to vegetation type, we computed the relative nestedness index C (Wright et al. 1990, Wright & Reeves 1992). We estimated statistical significance using Cochran's Q statistic (Wright & Reeves 1992). Values of C vary between 0 and 1.0, approaching 1.0 for perfectly nested matrices. Key advantages of this metric are that it allows for statistical comparison of degree of nestedness among matrices or data sets and is not highly sensitive to matrix size (Wright & Reeves 1992, Bird & Boecklen 1998). We used Z scores (standard-Normal variates) to test whether degree of nestedness was significantly

different between assemblages of butterflies associated with riparian versus non-riparian vegetation (Wright & Reeves 1992).

RESULTS

Of the 23 springs in the Spring Mountains that we surveyed, 21 included riparian vegetation and 20 included non-riparian vegetation. Eighteen springs included both riparian and non-riparian vegetation.

We observed a total of 55 species of butterflies at plots, at springs, and along springbrooks (Figure 1). All of the species were recorded in association with riparian vegetation; 37 species were recorded in association with non-riparian vegetation. Many of the 18 species that we recorded only in association with riparian vegetation are known to occur in non-riparian vegetation elsewhere in their distributional ranges. No species was recorded in association with non-riparian vegetation only. Species richness of butterflies at the spring level ranged from 7 to 30 (16.2 ± 6.2 , mean \pm SD). Species richness of butterflies in riparian vegetation fell between 6 and 30 (15.6 ± 6.5), and species richness in non-riparian vegetation ranged from 1 to 14 (8.2 ± 3.2).

We recorded a total of 4357 individual butterflies. Abundances of butterflies at the spring level ranged from 40 to 456 (189.0 ± 125.0 , mean \pm SD). Abundances of butterflies in riparian vegetation fell between 13 and 383 (154.4 ± 115.0), and abundances in non-riparian vegetation ranged from 3 to 136 (55.2 ± 35.2).

Across all springs, species richness of butterflies was significantly higher in riparian vegetation than in non-riparian vegetation ($F_{1,39} = 21.1$, $P < 0.001$). Within springs that had both riparian and non-riparian vegetation, the effect of vegetation category was significant as well ($t =$

4.119, $df = 17$, $P < 0.001$). Mean abundance of butterflies in riparian vegetation was significantly higher than in non-riparian vegetation, both across all sites ($F_{1,39} = 13.7$, $P < 0.001$) and within the 18 springs that contained both categories of vegetation ($t = 3.788$, $df = 17$, $P < 0.01$).

At the level of individual sampling points, species richness and abundance of butterflies also were significantly higher in locations with riparian vegetation than in locations with non-riparian vegetation (species richness: $F_{1,145} = 40.43$, $P < 0.001$; abundance: $F_{1,145} = 41.52$, $P < 0.001$). Thus, although vegetation in a higher proportion of the sampling points (sampled area) was categorized as riparian (0.55) than as non-riparian (0.45), this difference did not appear to explain the discrepancy in species richness and abundance of butterflies between riparian and non-riparian vegetation.

Similarity of species composition of butterflies decreased as the linear distance between springs increased (Table 1). Neither local presence of larval hostplants nor vegetation association of larval hostplants had a statistically significant effect on occurrence rate or abundance of individual species of butterflies.

The distributional pattern of butterflies at all springs, at riparian portions of springs, and at non-riparian portions of springs was significantly nested (Table 2); therefore, the butterfly faunas at relatively depauperate springs were statistically proper subsets of the species present at relatively species-rich springs. Relative nestedness of assemblages associated with riparian versus non-riparian vegetation was not significantly different, suggesting that vegetation type as categorized in this study to date does not have an important influence on the ability to predict the order of butterfly colonizations or extirpations (i.e., the order of species associated with riparian vegetation is no more or less predictable than the order of species associated with non-riparian vegetation).

DISCUSSION

Our results suggest that reductions in water availability and the extent of riparian vegetation at montane springs in the Mojave Desert are likely to reduce local species richness and abundance of butterflies. Across several levels of spatial resolution, species richness and abundance of butterflies consistently was higher in riparian vegetation than in non-riparian vegetation. This is not surprising given the importance of water, especially in xeric systems, for sustaining larval hostplants, adult nectar sources, and moist soil from which some species of butterflies draw water and nutrients (Nelson & Andersen 1999, Mac Nally et al. 2004). In semi-arid and arid environments, butterflies, like many other terrestrial taxa, rely heavily on resources provided by springs, spring-fed riparian systems, and other isolated wetlands (Shapiro 1984, Austin 1985, Murphy & Wilcox 1986, Schlicht & Orwig 1998). In addition, the structurally complex vegetation often characteristic of riparian areas creates refugia for many species of butterflies that cannot tolerate relatively hot or dry microclimates (Galiano et al. 1985).

Financial and logistic obstacles make it impossible to inventory terrestrial and aquatic taxonomic groups at each spring in the Spring Mountains. Accordingly, land managers would like to develop a method to predict measures of biodiversity as functions of readily categorized attributes such as land cover. Although species richness and abundance of butterflies appears to benefit from maintenance of riparian vegetation, our results indicate that the ability of broad categories of vegetation to serve as a predictor of species richness and composition of butterflies may be relatively low. In our study system, for example, neither local presence of larval hostplants nor vegetation association of larval hostplants was an effective predictor of occurrence rate or abundance of individual species of butterflies. We suspect that that observation at least in

part reflects a relatively high degree of polyphagy among the butterfly species encountered in this study, which may serve to reduce effective differences in the suitability of springs that differ substantially in the composition of their vegetation. Nonetheless species present in relatively depauperate locations tended to be subsets of the species present in locations that are richer in species, but the degree of order in species composition (i.e., the predictability of local extirpations and colonizations) did not appear to be affected by whether riparian habitat was available.

We recognize that conclusions drawn from one year of data on butterfly occurrence and abundance may not be definitive. We also acknowledge that the estimates of resource quantity and quality presented here are relatively coarse; we currently are collecting data on more-detailed measures of vegetation structure and composition that may have greater ability to predict the order of butterfly colonizations or extirpations. Nonetheless, absence of a tight link between occurrence of butterflies and occurrence of larval hostplants is not uncommon (Holl 1996, Waltz & Covington 2004). Although adults that are facultative or obligate nectarivores may be drawn to the high concentrations of flowering plants that can be characteristic of riparian areas, considerable proportions of the distributions of primary larval hostplants in arid environments, as well as entire distributions of potential alternative hosts, may occur beyond riparian boundaries (Galiano et al. 1985).

To some extent, the apparent inability of vegetation type to serve as an effective predictor of biodiversity patterns of butterflies may reflect the tremendous variation in abiotic and biotic attributes of springs in the Spring Mountains, including but not limited to area and morphology of the spring head and springbrook; water volume, chemistry, and seasonal variability; and disturbance history of disturbance from all sources (Wettstein & Schmid 1999). We have

observed similarly weak relationships between species richness and composition of aquatic invertebrates in the Spring Mountains and gradients in disturbance intensity and major environmental variables (Sada et al. in press). The isolation of an individual spring also appears to play an important role in determining its butterfly species composition; springs that are closer together tend to have more similar assemblages of butterflies than springs that are further apart.

One of several useful considerations in establishing location-specific priorities for conservation and rehabilitation is presence of ubiquitous or “weedy” species—in any taxonomic group—that are characteristic of biotic homogenization or are able to exploit specific natural and human disturbances as opposed to species characteristic of less disturbed locations (Noss 1990, Lockwood & McKinney 2001, McKinney 2002). In our study system, individual species of butterflies were present in one to 23 springs, with a median occurrence rate of six springs (6.8 ± 5.6 , mean \pm SD). The two species of butterflies present at all 23 springs surveyed, *Leptotes marina* and *Vanessa cardui*, are highly vagile as adult individuals, are geographically widespread, and often occur in locations subject to relatively intensive human land uses (Scott 1986). The third and fourth most prevalent species among the springs we surveyed, *Pontia protodice* and *Danaus gilippus*, likewise are fairly opportunistic. Our results, therefore, reinforce the principle that protection of locations that currently support a large number of species, while desirable and necessary for protection of biodiversity, may not be sufficient to meet all conservation goals. Even in a significantly nested system, some species that are absent from relatively species-rich locations are present in locations with equal or lower species richness. Establishment of conservation priorities and strategies requires not only information on species richness and abundance but also complementary measures of ecological condition and function (Kinzig et al. 2002).

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Figure 1. Species of butterflies present at 23 springs in the Spring Mountains. Springs are listed in decreasing order of species richness; species are listed in decreasing order of number of springs occupied. * indicates butterflies found only in association with riparian vegetation in this study (may occur in non-riparian vegetation elsewhere). Springs: A, Sawmill Spring; B, Willow Creek; C, Switchback Spring; D, Pine Creek; E, Cold Creek; F, La Madre Spring; G, Ash Creek; H, Lost Creek; I, Mountain Springs; J, Ice Box Canyon; K, Oak Creek; L, Bonanza-f; M, Bonanza-u; N, Calico Spring; O, Mud Spring 1; P, Mud Spring 2; Q, First Creek; R, Red Spring; S, Willow Spring; T, Wheeler Spring; U, White Rock Spring; V, Willow Seep; W, Calico Tanks. Butterflies: 1, *Leptotes marina*; 2, *Vanessa cardui*; 3, *Pontia protodice*; 4, *Danaus gilippus*; 5, *Anthocharis sara*; 6, *Hemiargus isola*; 7, *Eurema nicippe*; 8, *Colias eurytheme*; 9, *Junonia coenia*; 10, *Nathalis iole*; 11, *Pontia sisymbrii*; 12, *Danaus plexippus*; 13, *Vanessa annabella*; 14, *Adelpha bredowii*; 15, *Celastrina ladon*; 16, *Erynnis brizo*; 17, *Incisalia fotis*; 18, *Pyrgus communis**; 19, *Cercyonis sthenele*; 20, *Limenitis weidemeyerii*; 21, *Papilio polyxenes*; 22, *Chlosyne acastus neumogeni*; 23, *Colias cesonja*; 24, *Nymphalis antiopa**; 25, *Papilio indra*; 26, *Nymphalis californica*; 27, *Pontia beckerii*; 28, *Strymon melinus*; 29, *Erynnis meridianus**; 30, *Heliopetes ericetorum**; 31, *Megathymus yuccae*; 32, *Brephidium exile*; 33, *Hemiargus ceraunus*; 34, *Atlides halesus*; 35, *Euchloe hyantis**; 36, *Hesperia comma**; 37, *Icaricia acmon**; 38, *Pieris rapae**; 39, *Speyeria carolae*; 40, *Vanessa virginiensis**; 41, *Apodemia mormo*; 42, *Apodemia palmerii*; 43, *Euphilotes ancilla**; 44, *Mitoura siva**; 45, *Polygonia zephyrus*; 46, *Vanessa atalanta*; 47, *Chosyne acastus robusta**; 48, *Chlosyne californica**; 49, *Copaeodes aurantiaca**; 50, *Erynnis funeralis**; 51, *Everes amyntula*; 52, *Loranthomitoura spinetorum**; 53, *Nymphalis milberti**; 54, *Polygonia satyrus*; 55, *Satyrium behrii*

Table 1. Correlations between distance between springs and similarity of species composition of butterflies at all springs, the riparian component of springs, and the non-riparian component of springs. Values are Mantel r statistics. For all values, $P \leq 0.001$.

	Mantel's r	P
all springs	0.27	0.01
riparian vegetation	0.14	0.06
non-riparian	0.30	0.003

Table 2. Size and values of the relative nestedness index C for matrices that included all springs, the riparian component of springs, and the non-riparian component of springs.

Degrees of freedom are (number of species – 1). All P-values < 0.0001.

	sites	species	C
all springs	23	55	0.366
riparian	21	55	0.367
non-riparian	20	37	0.352

MANUSCRIPT #3

Response of spring-dependent aquatic assemblages to environmental and land use
gradients in a Mojave Desert mountain range

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INTRODUCTION

Springs and spring-fed aquatic systems historically have supported a substantial proportion of the aquatic and riparian species that inhabit the arid western United States (Fisher et al. 1972, Williams and Koenig 1980, Gubanich and Panik 1986, Myers and Resh 1999). Several hundred endemic species and subspecies of fishes, mollusks, crustaceans, aquatic insects, and plants depend on springs (Hubbs and Miller 1948, Minckley et al. 1986, Hershler 1998, 1999, Polhemus and Polhemus 2002, Smith et al. 2002). In addition, springs provide resources for numerous terrestrial species (Myers and Resh 1999). For example, approximately 80 percent of the terrestrial animal species in the Great Basin are facultative or obligate users of riparian systems (Thomas et al. 1979), including more than two-thirds of the nongame species of breeding birds (Saab et al. 1995).

Because springs provide the only reliable source of water across much of the western United States, human land uses also have tended to concentrate around springs. Human activities that alter water quality and vegetation cover include diversion of water for domestic and municipal use, livestock grazing, and recreation (Shepard 1993). Furthermore, both intentionally and inadvertently, humans have introduced numerous non-native species to springs (Hendrickson and Minckley 1984, Sada and Vinyard 2002). Grazing and trampling by feral horses and burros also modify the morphology and vegetation of springs. Accordingly, rates of extinction are higher for native species that occur in springs and spring-fed aquatic systems than for species associated with any other type of land cover in the western United States (Sada and Vinyard 2002).

When springs are either desiccated or degraded severely by natural or anthropogenic environmental change, their aquatic assemblages can be eradicated completely (Minckley and Deacon 1968, Johnson and Hubbs 1989, Sada and Vinyard 2002). The response of spring biotas to less severe and more pervasive disturbances, however, is poorly understood. Few standardized biological surveys of spring-fed riparian systems have been conducted, and most of those concentrated on springs that were minimally affected by disturbance.

In January 2001, the U.S. Fish and Wildlife Service (USFWS) issued the Clark County Multiple Species Habitat Conservation Plan (MSHCP). This 30-year permit to Clark County—the nation’s most rapidly urbanizing municipality, thanks to explosive growth of the Las Vegas metropolitan area—authorizes the incidental take (i.e., take resulting from otherwise lawful activities) of 79 species. Some 20 of these taxa are spring endemics, spring obligates, or primarily are associated with springs. Among the requirements of the MSHCP is development of a Conservation Management Plan for springs in the permit area. The Spring Mountains, an isolated mountain range in the eastern Mojave Desert that covers approximately 4000 km² and contains approximately 300 springs, has become a principal focus of these planning efforts. Because the majority of the Spring Mountains is under jurisdiction of the U.S. Forest Service and U.S. Bureau of Land Management, prioritization of its springs for conservation and rehabilitation has considerable management relevance.

Financial and logistic obstacles make it impossible to inventory the status of the aquatic biota of each spring in the Spring Mountains. Accordingly, managers would like to develop a method to predict species richness and composition using easily measured

environmental gradients and estimates of disturbance intensity. These predictions, in turn, could be used to rank springs for different types of land use and management actions. To examine whether such predictions are feasible, we surveyed aquatic assemblages at 45 springs. First, we tested whether species richness, evenness, and species composition varied as a function of disturbance intensity. Because the response of many aquatic taxa to disturbances is similar regardless of the source of those disturbances, our estimate of disturbance intensity included both natural events and human land use (including use of springs by feral ungulates). Second, we investigated whether species richness and evenness could be explained using five different environmental variables that reasonably might be expected to have an influence on diversity of aquatic animals: spring elevation, spring discharge, springbrook length, water temperature, and electrical conductance. In general, species richness is expected to increase as elevation, discharge rate, and length increase. Species richness is expected to be correlated negatively with water temperature and electrical conductance (concentrations of dissolved solids). Third, we used nestedness analyses to test whether species richness and composition were predictable with respect to alternative environmental criteria and whether disturbance intensity was associated with the degree of order of species presences and absences.

METHODS

Study system

The Spring Mountains are ca 125 km long and span an elevational gradient from 1500 m in Las Vegas Valley to 3632 m on Charleston Peak. As elevation increases, annual precipitation increases from less than three cm to more than 55 cm. Summer

temperatures may reach 46° C at the lower end of the elevational gradient, decreasing to – 9° C at relatively high elevations during the winter (Hidy and Klieforth 1990).

Most of the springs in the Spring Mountains are small and isolated, and many have been excavated or otherwise developed. Diversion structures, such as spring boxes to collect water and pipes to transport water to nearby troughs or tanks, are common. Numerous non-native species (mostly plants and fishes) have colonized these springs, and many springs are impacted by stochastic phenomena such as fire, avalanche, and flood. Nonetheless, some springs appear to be in good condition and have been minimally affected by either natural or anthropogenic disturbance.

Field methods

During summer 1995, we sampled 45 springs that collectively spanned abiotic and disturbance gradients in the Spring Mountains. Biological surveys focused on spring sources and the springbrook immediately downstream. The entire spring area was sampled when the length of the springbrook was less than 50 m. At more extensive springs, surveys were constrained to upstream reaches with a distinctive riparian assemblage. Physical and chemical characteristics were recorded at the spring source and approximately 50 m downstream of the source.

Disturbance intensity at each spring was categorized as undisturbed, slightly disturbed, moderately disturbed, or highly disturbed. Because aquatic assemblages have similar responses to reduction in habitat quality regardless of its cause, we did not discriminate between natural and anthropogenic disturbances. Undisturbed springs appeared to be unaffected by historical or recent human land use, and slightly disturbed

springs had little evidence of vegetation or soil disturbance. It was impossible to determine whether springs in the latter two categories never had been disturbed or whether they had reached an alternative stable state following historical disturbances. Recent disturbance was evident at moderately disturbed and highly disturbed springs. We categorized springs with vegetation covering > 50% of their banks and at least 50% of natural discharge remaining in diverted spring brooks as moderately disturbed. Springs with vegetation covering < 50% of their banks, that contained < 50% of natural discharge, or were either impounded, dredged, or recently disturbed by natural events were categorized as highly disturbed. Ephemeral springs were categorized as highly disturbed because of recent flow reduction.

Temperature and electrical conductance were measured with YSI Model 57 and 33 meters, respectively. Grab samples of aquatic macroinvertebrates were collected by roiling substrates and capturing material that washed downstream with a 250-micron mesh net. All aquatic habitat types (e.g., banks, mid-channel, gravel, sand, cobble, boulder, bedrock, emergent and submerged aquatic vegetation) were sampled for approximately 20 minutes at each spring. Samples were immediately fixed in 10 percent formalin and transferred to 75 percent ethyl alcohol for preservation. Samples were sorted, identified, and enumerated in the laboratory. Many groups were identified to genus (some to species); dipterans (flies) were identified to family. Crustaceans (ostracods, brachiopods, amphipods, and isopods), oligochaets, nematodes, and mites were identified as such.

Analyses

We used analysis of variance to test whether species richness and evenness varied as a function of disturbance intensity. When there was a significant effect of disturbance, we used least-squared differences to compare categories. To examine spatial variation in species composition, we calculated dissimilarity of species composition between pairs of springs using Bray-Curtis distances. We used non-parametric multivariate analysis of variance (NPMANOVA, Anderson 2001; McArdle and Anderson 2001) to test whether community dissimilarity differed among disturbance categories.

We used linear regression to test whether species richness and evenness could be explained as a function of spring elevation, spring discharge, springbrook length, water temperature, or electrical conductance. We quantified evenness as $E = e^H/S$, where $H = -\sum p_i \ln(p_i)$, p_i is the proportion of individuals found in the i th species, and S is the number of species in the site (Hayek and Buzas 1997). E ranges from 0 to 1, approaching 1 when individuals are partitioned equally among species.

To test whether species richness and composition were predictable with respect to alternative environmental criteria, we used nestedness analyses. Nestedness analyses have greatly expanded our capacity to understand biotic patterns across networks of terrestrial or aquatic “islands” (Wright et al. 1998). A nested biota is one in which the species present in relatively depauperate locations are subsets of the species present in locations that are richer in species (Patterson and Atmar 1986). Nestedness is a property of assemblages or communities, not of individual species (Wright et al. 1998), and has been interpreted as a measure of biogeographic order in the distribution of species (Atmar and Patterson 1993).

Numerous studies have demonstrated nested distributional patterns are common across taxonomic groups and ecosystems. Biotas rarely are perfectly nested, however. Nestedness analyses often cannot identify critical thresholds of environmental variables with respect to system state or reliably predict the order of species extirpation or colonization. Nonetheless, nestedness analyses are useful as tools for land management because they can quantify widespread ecological patterns and—more importantly—highlight processes, including nonrandom extinction, differential colonization, and nestedness of critical resources, which affect not only species richness, but also species composition (Patterson and Atmar 1986, Simberloff and Martin 1991, Cook and Quinn 1995, Lomolino 1996, Baber et al. in press). Although even strong correlations between mechanisms or environmental variables and distributional patterns cannot be interpreted as cause-and-effect relationships, those correlations can, at minimum, help refine hypotheses, which can be tested with further manipulative experiments or observations (Cook and Quinn 1995, Kadmon 1995, Fleishman and Mac Nally 2002). This aspect of nestedness analysis is especially pertinent in conservation planning, because it may help to elucidate whether certain land uses are responsible for local extinctions or colonizations (Hecnar and M'Closkey 1997, Fleishman and Murphy 1999, Jonsson and Jonsell 1999).

Presence / absence matrices for nestedness analysis typically are assembled by listing locations in order of decreasing species richness as rows and species in order of decreasing ubiquity as columns. This ordering provides a description of assemblage composition but contributes little toward understanding agents that determine assemblage structure and help us to predict species composition across space and time. If one wishes

to test whether a particular environmental variable may be related to a nested distributional pattern, then rows instead may be ordered with respect to that variable (Fleishman and Mac Nally 2002). For example, listing rows in order of decreasing area quantifies the degree to which biotas are nested by area. If an assemblage is nested with respect to a selected environmental variable—or if an assemblage is more nested with respect to one environmental variable than another—it suggests that the variable in question has a non-trivial influence on species occurrence in the assemblage.

To test whether assemblages were nested with respect to elevation, discharge, springbrook length, water temperature, and electrical conductance, we computed the relative nestedness index C (Wright and Reeves 1992) with the program NESTCALC (Wright et al. 1990). We estimated statistical significance using Cochran's Q statistic (Wright and Reeves 1992). Values of C vary between 0 and 1.0, approaching 1.0 for perfectly nested matrices. A key advantage of this metric is that it allows for statistical comparison of degree of nestedness among matrices or data sets. Moreover, C is not highly sensitive to matrix size (Wright and Reeves 1992, Bird and Boecklen 1998), although nestedness may be more variable when matrices are relatively small (Wright et al. 1998). We used Z scores (standard-Normal variates) to test whether significant differences existed in relative nestedness among matrices ranked by different environmental criteria (Wright and Reeves 1992). We also tested whether degree of nestedness was significantly different between springs in different disturbance categories.

RESULTS

The species richness of our 45 study springs ranged from three to 13 (mean 6.2 ± 2.5 SD). Forty-eight taxa were recorded; individual taxa were present in one to 40 springs. Spring-level evenness fell between 0.01 and 0.25 (mean 0.07 ± 0.05 SD). Complete data are available from the corresponding author on request.

Ten springs were categorized as undisturbed. The number of springs categorized as slightly disturbed, moderately disturbed, and highly disturbed was 10, 9, and 16, respectively. Sampled springs covered an elevational gradient from 1082 to 3097 m. Rates of discharge ranged from 0 to 870.3 l/min. Springbrook length fell between 0 and 5000 m. Water temperatures were between 3.3°C and 25°C, and electrical conductance ranged from 210 to 1950 umhos/sec.

Effect of environmental variables on species richness and evenness

Species richness varied as a function of disturbance intensity ($F_{3,41} = 3.20$, $P < 0.05$, Figure 1). Species richness was significantly greater at slightly disturbed springs than at highly disturbed springs ($P < 0.01$). Species richness also was greater (although not significantly so) at slightly disturbed and moderately disturbed springs than at either undisturbed or highly disturbed springs (Figure 1). Evenness did not vary as a function of disturbance category.

Mean dissimilarities (Bray-Curtis distances) of species composition between pairs of springs ranged from a minimum of 61.82 ± 20.22 SD between pairs of undisturbed springs to a maximum of 71.46 ± 16.09 SD between pairs of highly disturbed springs. Dissimilarity values did not increase monotonically as disturbance intensity increased;

dissimilarity of species composition was greater between slightly disturbed springs than between moderately disturbed springs. Differences in dissimilarity of species composition among disturbance categories were not statistically significant ($F_{3,44} = 0.80$, $P = 0.73$). Comparison of species composition between pairs of springs in different disturbance categories also revealed little variation in dissimilarity values. Mean dissimilarity was lowest between undisturbed and moderately disturbed springs (64.19 ± 17.45 SD) and greatest between slightly disturbed and highly disturbed springs (69.46 ± 16.72 SD).

Neither elevation, water temperature, nor electrical conductance had a significant effect on species richness. When all 45 springs were included in the analyses, species richness increased significantly as discharge increased ($F_{1,44} = 10.15$, $P < 0.01$, $R^2 = 0.19$) and as springbrook length increased ($F_{1,44} = 13.63$, $P < 0.001$, $R^2 = 0.20$). Two springs, however, had both unusually high rates of discharge and long springbrooks. Discharge rates for these two springs were 870.3 and 851.4 as compared with a mean of 24.9 ± 29.6 SD and maximum of 189.2 for the other 43 springs; springbrook lengths were 5000 and 4000, compared with a mean of 475.9 ± 673.1 and a maximum of 2000 for the other 43 springs. When these two springs were excluded from the analyses, neither discharge ($F_{1,41} = 1.00$, $P = 0.32$) nor springbrook length ($F_{1,41} = 1.39$, $P = 0.25$) had a statistically significant effect on species richness. None of the five environmental variables had a statistically significant effect on evenness.

Nestedness

The distributional pattern of aquatic invertebrates was significantly nested regardless of whether matrix rows were ordered by species richness, elevation, discharge, springbrook length, water temperature, or electrical conductance (Table 1). Therefore, the invertebrate faunas in relatively depauperate sites were statistically proper subsets of the species present in relatively species-rich locations. The matrix ordered by species richness was significantly more nested than matrices ordered by any other environmental variable (Table 2). This result is not very surprising, nor is it highly informative for understanding variables associated with species richness patterns or for land-use planning. The more important and potentially useful result is that there were no significant differences in the relative nestedness of species ordered by other environmental criteria (Table 2). In other words, the relative influence of elevation, discharge, springbrook length, water temperature, and electrical conductance on overall patterns of species richness and composition appeared to be approximately equal.

There were no significant differences in relative nestedness between springs in different disturbance categories (Table 3), suggesting that the potential of disturbance to predict patterns of assemblage structure may be limited.

DISCUSSION

Because it is not feasible to develop priorities for conservation and management action using detailed biological inventories of each spring in the Spring Mountains, we examined whether species richness, evenness, and composition could be predicted as a function of disturbance intensity or relatively straightforward, repeatable measures of

major environmental gradients. In general, springs and other isolated wetlands offer an excellent opportunity to examine the impact of disturbance processes on aquatic assemblages (Hecnar and M'Closkey 1996, Baber et al. in press). These systems are easily delineated in space, and typically function as islands of habitat. Moreover, assemblages of aquatic invertebrates largely are influenced by disturbance events. In ephemeral wetlands, for example, desiccation stress is expected to exert a dominant influence over species richness and composition (Wellborn et al. 1996).

Our results suggest that species richness of aquatic macroinvertebrates in the Spring Mountains may be greatest at intermediate levels of disturbance. Species richness was significantly greater at slightly disturbed springs than at highly disturbed springs, and tended to be greater at slightly disturbed and moderately disturbed springs, than at either undisturbed or highly disturbed springs. Numerous studies have demonstrated that species richness may have a predictable response to gradients of natural disturbance and human disturbance, including activities associated with urbanization (Mackin-Rogalska et al. 1988, Kowarik 1995, Denys and Schmidt 1998, McIntyre 2000, Blair 2001, Pickett et al. 2001); the functional form of the response often depends on the spatial resolution and extent of observation and whether species have adapted to a particular disturbance over evolutionary time. Along an urbanization gradient, for example, species richness often peaks in locations with an intermediate degree of urban development (Blair 1999). In many systems, however, a high proportion of the species found in locations with intermediate levels of urbanization are relatively ubiquitous native or non-native taxa. Many species with narrow resource requirements, by contrast, are restricted to locations with relatively little urban development despite the fact that the latter locations tend to

have lower species richness than sites with some urban development (McKinney 2002). Baber et al. (in press) found that ephemeral wetlands in the northeastern United States were used by several aquatic species of conservation concern that often did not occur in larger and more permanent wetlands with greater species richness.

Water diversion and other human land uses are among the dominant stressors in riparian areas in the arid western United States (Kauffman and Krueger 1984, Armour et al. 1991, Dobkin and Rich 1998). As this study demonstrated, however, distribution patterns of faunal assemblages do not always reflect the effects of those stressors—or do not reflect the effects in a predictable manner. For example, livestock grazing, recreation, and other activities that reduce water availability and degrade riparian vegetation had little detectable effect on nestedness of butterflies and birds in the Great Basin (Fleishman et al. 2002). At least three explanations seem plausible (Fleishman and Murphy 1999). First, disturbance intensity in wetlands may not be sufficiently severe to cause local extirpations. Second, taxa that are particularly vulnerable to changes in the structure and species composition of wetlands may already have disappeared. Third, the magnitude of disturbance may not be arranged in a predictable (nested) manner across the region (Hecnar and M'Closkey 1997).

Although our results should not be interpreted to mean that elevation, discharge, springbrook length, water temperature, and electrical conductance have no effect on species richness and composition, the ability of these variables to serve as predictors of species richness and composition may be relatively low. Species present in relatively depauperate locations tended to be subsets of the species present in locations that are richer in species, but that pattern did not appear to be driven by either the environmental

variables we measured or by disturbance intensity. Our results may simply reflect the tremendous variation in spring area, morphology, water chemistry, and disturbance history in the Spring Mountains. Springs are influenced by regional and local geology, climate, and groundwater hydrology (Freeze and Cherry 1979, McCabe 1998). In the Spring Mountains, some springs dry each year, some dry only during extended droughts, and some persist for millennia. This range of conditions is echoed by the diversity of aquatic taxa that inhabit springs, including many crenobiotic invertebrates and vertebrates with restricted geographic distributions (Resh 1983, Cushing 1996, Shepard 1992, Wiggins and Erman 1987). Our results are similar to those of Heino et al. (2003), who found that macroinvertebrate taxa inhabiting boreal streams—many of which, like wetlands in the Spring Mountains, are characterized by frequent, unpredictable disturbances—tended to exhibit individualistic, taxon-specific responses to environmental gradients.

Ideally, ecologists and land managers would be able to predict how environmental and land use changes will affect values of species richness, patterns of local extirpation and colonization, and other biodiversity metrics. The ability to make reliable predictions would increase the scientific information base for decision-making and simplify development of conservation and land use plans. Our work suggests that spring-fed aquatic assemblages in the Spring Mountains cannot be characterized easily along existing gradients that may seem pronounced to the human eye, such as drought (whether from stochastic weather patterns or water diversion) and livestock grazing. Manipulate experiments might increase our ability to understand how spring assemblages respond to

some types of disturbance, but unfortunately such experiments often prove difficult to implement on federal lands.

Again, we emphasize that lack of predictive ability is not synonymous with lack of effect. Nor is it impossible to prioritize springs for conservation and rehabilitation on the basis of other ecological and socioeconomic criteria. For example, related work on plants suggests that number of native species declines as disturbance intensity increases, whereas number of non-native species is greatest at an intermediate level of disturbance. Water diversion clearly affects the function of riparian systems independent of its effects on aquatic macroinvertebrates, and high densities of feral ungulates near springs tend to reduce aesthetic appeal. We hope our work will encourage ecologists and practitioners to consider a diverse range of biological and management-related values and implement innovative conservation solutions.

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Table 1. Size and values of the relative nestedness index C for (a) matrices with rows ordered by different environmental criteria or (b) matrices that included springs in different disturbance categories (ordered by species richness). Degrees of freedom are (number of species – 1). All P-values < 0.0001.

row order	springs	taxa	C
species richness	45	48	0.324
elevation	45	48	0.236
discharge	45	48	0.258
springbrook length	45	48	0.266
water temperature	45	48	0.239
electrical conductance	45	48	0.232
disturbance category	springs	taxa	C
undisturbed	10	24	0.228
slightly disturbed	10	33	0.156
moderately disturbed	9	26	0.232
highly disturbed	16	30	0.204

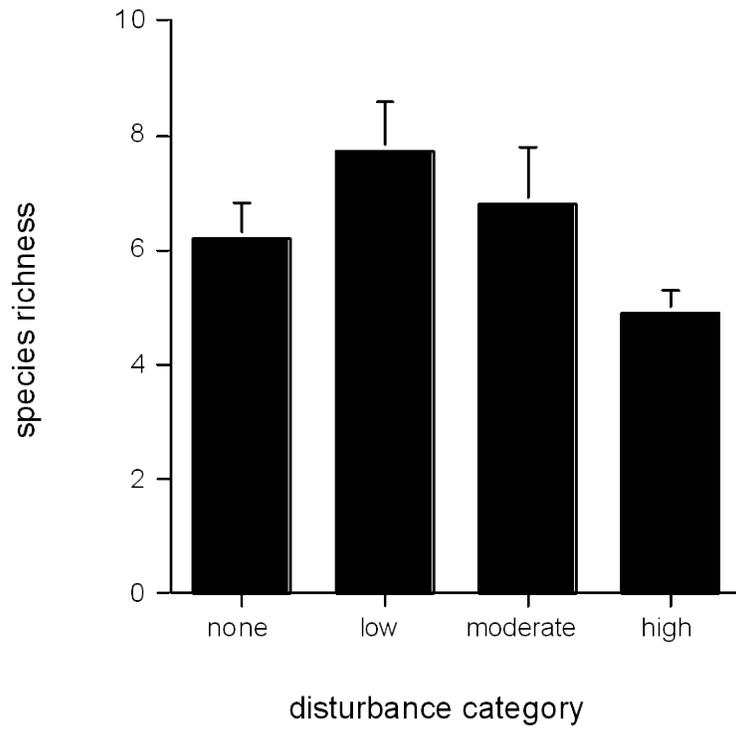
Table 2. Relative nestedness of aquatic invertebrates. Values are one-tailed *Z*-scores for matrices ordered by different criteria. *** $P \leq 0.001$, ** $P < 0.01$, * $P < 0.05$. Values represent the relative nestedness of the row versus the column; positive values indicate higher nestedness and negative values indicate lower nestedness (for example, the matrix ordered by elevation was less nested than the matrix ordered by discharge). *S*, species richness; elev, elevation; length, springbrook length; temp, water temperature; EC, electrical conductance.

	S	elev	discharge	length	temp	EC
S		3.31***	2.47**	2.18*	3.19***	3.42***
elev	-3.31***		-0.83	-1.12	-0.12	0.12
discharge	-2.47**	0.83		-0.29	0.72	0.95
length	-2.18*	1.12	0.29		1.01	1.24
temp	-3.19***	0.12	-0.72	-1.01		0.24
EC	-3.42***	-0.12	-0.95	-1.24	-0.24	

Table 3. Relative nestedness of aquatic invertebrates as a function of disturbance intensity. Values are one-tailed *Z*-scores. Values represent the relative nestedness of the row versus the column; positive values indicate higher nestedness and negative values indicate lower nestedness.

	undisturbed	slightly disturbed	moderately disturbed	highly disturbed
undisturbed		0.25	-0.02	0.11
slightly	-0.25		0.01	0.13
moderately	0.02	-0.01		0.12
highly	-0.11	-0.13	-0.12	

Figure 1. Mean species richness of aquatic invertebrates as a function of disturbance intensity. Error bars are standard error.



MANUSCRIPT #4

Temporal sampling considerations for aquatic invertebrates for use in monitoring schemes in support of conservation management (in progress)

Erica Fleishman, Donald Sada, and Dennis Murphy

Methods

Aquatic macroinvertebrates were sampled between June and August 2004 at 16 springs that collectively span major environmental and land-use gradients in the Spring Mountains. Each spring was visited once per month for a total of three visits. Samples were sorted and identified in the laboratory. Many groups were identified to genus and some to species. For simplicity, we refer to the taxa recorded at each spring as “species.”

Species were categorized by behavior and functional feeding group. We recognized five behavioral categories: burrower, climber (climbs on aquatic vegetation), clinger (clings to rocks, may be a very good crawler), sprawler (sprawls on soft sediments, good at staying unburied), and swimmer. We also recognized five functional feeding groups: collector–filterer (uses a net-like apparatus to catch small particles drifting on the current), collector-gatherer (collects all manner of small particles), predator (eats other aquatic macroinvertebrates), scraper (scrapes algae off surfaces), and shredder (shreds plant material, usually decaying leaves).

We measured similarity of species composition among months at a given spring with the Jaccard index, $C_j = j / (a+b-j)$, where a is the number of species in the first sample, b is the number of species in the second sample, and j is the number of species

shared among samples. We used simple linear regression to examine whether species richness across the season could be explained as a function of species richness in a given month. We used Spearman rank correlation to explore whether the order of springs by species richness was similar in a given month and across the season. We used analysis of variance to examine whether prevalence (number of springs at which a species was detected) or proportion of visits at which a species was detected varied as a function of behavior or functional feeding group. When there was a significant effect of behavior or functional feeding group, we used least-squared differences to compare categories.

Results

We recorded a total of 155 species of aquatic macroinvertebrates, representing 49 families. Species richness of aquatic macroinvertebrates at our 16 study springs ranged from ten to 38 (24.4 ± 7.5 , mean \pm SD). Individual species were present at one to 11 springs; most species were detected at few springs (2.5 ± 2.4 , mean \pm SD).

The mean number of species recorded at a spring was relatively similar among months, but each of the three monthly samples underrepresented species richness across the season (Table 1).

Few species were detected in all three monthly samples. The proportion of visits at which a given species was detected, averaged across all springs at which the species was present, fell between 0.33 and 1.00 (0.43 ± 0.16 , mean \pm SD). At no spring was the proportion of taxa detected at all visits greater than 0.33, and at some springs no species was detected at all visits (mean across springs: 0.16 ± 0.10).

Similarity of species composition (C_j) between pairs of monthly samples was low. Between June and July, C_j ranged from 0–0.46 (mean across springs: 0.27 ± 0.13). Between July and August, C_j ranged from 0.08–0.53 (mean across springs: 0.28 ± 0.15). Similarity of species composition between the June and August samples did not exceed 0.43 (minimum = 0.11, mean across springs: 0.25 ± 0.11).

Species richness in any one month explained a statistically significant proportion of variance in species richness across the season (Table 2). The ranking of springs with respect to species richness in a given month was similar to the rank across the season (Table 2).

Prevalence of species did not vary as a function of behavioral category. Prevalence did vary as a function of functional feeding group ($F_{4,133} = 3.49$, $P < 0.01$). Prevalence of collector–filterers and collector–gatherers was greater than prevalence of predators or shredders.

Proportion of visits at which a species was detected varied as a function of both behavior ($F_{4,136} = 2.65$, $P < 0.05$) and functional feeding group ($F_{4,133} = 5.82$, $P < 0.001$). Clingers were detected more consistently than burrowers, climbers, or sprawlers. Scrapers and shredders were detected more consistently than collector–gatherers, and all three were detected more consistently than predators.

Table 1. Species richness of monthly samples and their representation of species richness across the season at 16 springs in the Spring Mountains.

Month	Number of species			Proportion of season total		
	minimum	maximum	mean \pm SD	minimum	maximum	mean \pm SD
June	6	23	12.3 \pm 5.3	0.32	0.76	0.51 \pm 0.14
July	4	19	12.6 \pm 5.5	0.14	0.69	0.52 \pm 0.15
August	1	21	11.3 \pm 4.9	0.10	0.71	0.46 \pm 0.16

Table 2. Relationships between species richness in a given month and across the season at 16 springs in the Spring Mountains. *, $P < 0.05$, **, $P < 0.01$, ***, $P < 0.001$. R_S , Spearman rank correlation.

Month	$F_{1,15}$	R^2	R_S
June	15.67**	0.53	0.799**
July	14.92**	0.52	0.682**
August	20.09***	0.59	0.741**

MANUSCRIPT #5

Distribution of plants and animals in Spring Mountains spring and springbrook environments: using physical and biotic predictors of species presence to inform conservation planning (in progress)

Erica Fleishman, Ralph MacNally, Dennis Murphy, Todd Esque, and Donald Sada

Field Methods

Between April and August 2003, we conducted surveys of butterflies at 23 springs that collectively span major environmental and land-use gradients in the Spring Mountains. Visits were conducted once per month for a total of five visits per spring. Surveys were conducted when weather conditions were most conducive to flight (e.g., mostly sunny, light winds, warm temperatures). We detected a total of 55 species of butterflies (Fleishman et al. 2005).

Aquatic macroinvertebrates were sampled between June and August 2004 at 13 of the springs for which butterfly data were available. Each spring was visited once per month for a total of three visits. Samples were sorted, identified, and enumerated in the laboratory. Many groups were identified to genus and some to species. For simplicity, we refer to the taxa recorded at each spring as “species.” We detected a total of 168 species of aquatic macroinvertebrates.

Plants were sampled at 17 of the springs for which butterfly data were available. In most cases, springs were visited in spring and summer 2005. Our analyses also

incorporated data available from previous work in 2003 (Fleishman et al. 2006) and ongoing work in early 2006.

We used several complementary methods to characterize riparian vegetation at each spring. We recorded the identity, height (m), and diameter at breast height (cm) of all trees present within 10 m on either side of a 30 m line centered on and running downstream from the spring source and springbrook. Trees were defined as woody vegetation > 2 m in height with a single main trunk and canopy extending over the spring. We also recorded all species of understory plants that occurred within this area.

To further detect riparian species in all structural layers, we used a point-line-intercept method (Elzinga et al. 1998). Starting at the spring source and at each one-meter interval along the 30 m centerline (see above), we identified all species of plants that intersected the line, including overhanging trees and shrubs, understory forbs and grasses, and emergent or submergent aquatic species. We also sampled all species except trees in eight 0.10 m² quadrats. On the right side of the line, we placed quadrats 0.5 m away from the springbrook at 3 and 18 m downstream, and 3 m away from the springbrook at 6 and 21 m downstream. On the left side of the line, we placed quadrats 0.5 m away from the springbrook at 9 and 24 m downstream, and 3 m away from the line at 12 and 27 m downstream.

To characterize upland vegetation at each spring, we again used several complementary methods. To detect perennial species, we established eight 25 m line-intercept transects perpendicular to the springbrook. Transects were located at 0, 5, 15, and 30 m downstream on either side of the springbrook. The near-springbrook end of each transect was placed approximately 20 m away from the springbrook. Along each

transect, we recorded each perennial species, woody or herbaceous, that intersected the line. We recorded the identity, height, and diameter at either breast height or root collar of all trees that were present between the transects placed at 5 m and 15 m downstream on either side of the springbrook. Thus, upland trees at each spring were sampled in an area $\sim 500 \text{ m}^2$.

To further detect annual upland species, we recorded all taxa present in a total of twenty-four 1 m^2 quadrats. Three quadrats were placed along each line-intercept transect at distances of 0, 10, and 20 m from the near-springbrook end of the transect. We also recorded the identity of all species present between the transects placed at 15 and 30 m downstream on either side of the springbrook (total 1500 m^2).

We recorded a total of 343 species of plants, 113 in riparian areas and 284 in uplands (some species were present in both riparian areas and uplands). Complete lists of all species of plants, aquatic macroinvertebrates, and plants detected are available from E.F.

Overall disturbance at each spring was classified as none, low, moderate, or heavy. This composite measure of disturbance was based on the magnitude of fencing or water diversions, grazing by native and feral ungulates (cattle, elk, and feral horses and burros), and recreational impacts such as hiking, camping, and day use.

Geographic coordinates of each spring were measured with a global positioning system. At each spring, we also measured ten environmental variables that reasonably could be expected, a priori, to have an effect on turnover of butterflies or aquatic macroinvertebrates among springs: elevation (m), mean watered width of springbrook (cm), mean estimated percent shading of each spring by vegetation, mean water depth

(cm), mean water velocity (cm / sec), maximum water velocity (cm / sec), mean substrate size (mm); mean depth of vegetative detritus (cm), mean depth of submergent aquatic vegetation (cm), and mean springbrook length (m).

Analyses

To assess degree of turnover of butterflies, aquatic macroinvertebrates, and plants among springs we quantified pairwise dissimilarity of species composition, measured as Bray–Curtis distance. We quantified turnover for all aquatic macroinvertebrates, for relatively mobile aquatic macroinvertebrates (Odonata, Plecoptera, and Ephemeroptera), and for relatively sedentary macroinvertebrates (all other taxa). We quantified turnover for all species of plants, for plants detected in riparian areas, and for plants detected in uplands.

We used a modified version of Generalized Dissimilarity Modelling (GDM, Ferrier et al. unpublished ms) to examine relationships among turnover of butterfly species or aquatic macroinvertebrates, geographic separation, and environmental variables. The main difference between our implementation of GDM and that described by Ferrier et al. is that we added site-level random effects to account for the correlations among pairwise measures of dissimilarity of species composition. We also fit models within a Bayesian framework. Both of our modifications have advantages, particularly when sample sizes are small. The inclusion of site-level error terms explicitly models interdependencies within the dissimilarity matrix, allowing more meaningful estimates of uncertainty about model parameters and reducing the risk that a small number of sites will have undue influence on statistical inferences. Bayesian methods provide a coherent

theoretical and practical framework for fitting complex models with random effects, dealing with uncertainty of models and data, and accommodating small sample sizes and missing data.

We assumed a beta distribution for the response variable, parameterized as a mean response (μ) with a precision parameter (θ). A beta distribution so parameterized seems most appropriate for modelling dissimilarity data because the distribution is bounded by 0 and 1 and has variance function $\text{var}(y) = \mu(1-\mu)/(1+\theta)$, which is similar to that suggested by Ferrier et al. We used the same link function as Ferrier et al., $-\log(1-\mu)$.

The general model used for analyses was

$$\begin{aligned}
 S_{ij} &\sim \text{beta}(a_{ij}, b_{ij}) \\
 a_{ij} &= \mu_{ij} \theta \\
 b_{ij} &= (1 - \mu_{ij}) \theta \\
 -\log(1 - \mu_{ij}) = \eta_{ij} &= \alpha + \sum_{k=1}^K f_k(d_{kij}) + \sum_{l=1}^L |f_l(x_{li}) - f_l(x_{lj})| + \varphi_i + \varphi_j \\
 \text{var}(y) &= \frac{\mu(1-\mu)}{1+\theta}
 \end{aligned}$$

where $f(d)$ is a monotone transformation of a distance measure and $f(x)$ is a monotone transformation of an environmental variable. Note that η , and therefore all model parameters, must be non-negative for μ to be defined under the assumed beta distribution. This constraint was imposed by specifying appropriate prior distributions for model parameters (see below).

Spatial models

We regressed turnover of butterflies, all aquatic macroinvertebrates, mobile aquatic macroinvertebrates, and sedentary aquatic macroinvertebrates against distance between springs using GDMs of the form outlined above. We used cubic *I*-splines with positive coefficients to fit the monotonic transforming functions f to each covariate (Ferrier et al.). All models were fitted by Markov Chain Monte Carlo in the WinBUGS software package. The *I*-spline basis functions were calculated in *R* and transferred to WinBUGS as data. The coefficients for each spline f_k were drawn from a half-normal prior distribution with variance σ_k^2 , where σ_k is a hyper-parameter that governs the complexity of the fitted function. We gave each σ_k a flat uniform prior, so the shape of the fitted function was driven by the data.

To ensure η is positive, which is necessary for μ to be defined given the link function and beta response distribution, we “hierarchically centered” the random effects, giving them half-normal prior distributions with mean $\alpha/2$ and variance σ_{site}^2 , where α is the model intercept. α was given a half-normal prior with mean 0 and variance 10000. σ_{site} was given a flat uniform prior. σ_{site} is proportional to the amount of variation in species turnover that is not explained by the covariates but is associated with particular sites. We gave the dispersion parameter, θ , an flat uniform prior. We re-fitted models with different prior specifications for variance parameters and θ , including inverse-gamma, half-Cauchy, and flat uniform priors, and found virtually no differences in the resulting posterior distributions for parameters of interest.

We used the deviance information criterion (DIC, Spiegelhalter et al.) to assess model complexity and fit. The DIC is analogous to Aikake’s information criterion but is more appropriate for hierarchical Bayesian models. DIC is calculated as $DIC = \bar{D} +$

pD, where \bar{D} is the posterior mean of the deviance and pD is the effective number of parameters, defined as the posterior mean of the deviance minus the point estimate of the deviance evaluated at the posterior mean of the parameters. The model with the smallest DIC is estimated to be the model that best would predict a replicate data set of the same structure as the data set currently observed. For each taxonomic group we compared the DIC values of the regression models to that of a null model. The null model included only an intercept and the site-specific error terms. We considered only models with lower DIC values than corresponding null models to be supported by the data. Because DIC penalizes model complexity, the use of cubic splines might unnecessarily inflate DIC values in cases where a linear relationship on the link scale would be sufficient.

Therefore, we also fitted models with simple linear transformations of covariates. DIC values for linear models were either greater than or only marginally lower (< 1.5 units) than values for corresponding *I*-spline models, and never were lower than corresponding null model DIC values unless the *I*-spline model also had lower DIC value than the null model. Inclusion of a covariate with cubic transformation does not necessarily increase the number of effective parameters by three, because the three coefficients are treated as random variables from a common distribution.

We calculated pseudo- R^2 values for fitted *I*-spline models as the square of the sample correlation between $g(y)$ and η , where $g(\cdot)$ represents the link function (REF). Because η includes the site-level error terms, or variation that is associated with particular sites but otherwise is unexplained, overall R^2 values do not necessarily indicate the relative proportions of variation associated with model covariates. We therefore calculated a covariate-only pseudo- R^2 , which we denote R_c^2 , using only the covariate

component of η , which we denote η' . That is, $\eta'_{ij} = \eta_{ij} - (\psi_i + \psi_j)$, and R_c^2 is the squared correlation between $g(y)$ and η' .

Influence of plant assemblages

To investigate the possible influence of plant assemblages on species composition of invertebrates, we examined the relationships between turnover of butterflies or aquatic macroinvertebrates and turnover of plant species using correlation and regression analyses. We first examined the rank correlation between each invertebrate dissimilarity matrix and the three plant similarity matrices (all plant species, riparian plant species, and upland plant species). We then fitted GDMs to each group of invertebrates using as a predictor variable the plant dissimilarity matrix that had the highest rank correlation with that group of invertebrates. We also fitted models that included both geographic separation and plant dissimilarity as predictors of invertebrate dissimilarity. Models were compared using DIC and pseudo R^2 values as described above.

We used Bayesian model selection to determine which variables were the most likely predictors of turnover for each group of invertebrates. Bayesian model selection is based on the posterior probabilities of models, which represent the degrees of belief in particular models given the data and any prior beliefs (Raftery et al. 1997, Wintle et al. 2003). The use of Markov Chain Monte Carlo avoids the burden of calculating the posterior probabilities of all possible models by simulating a sample from the joint posterior distribution (George and McCulloch 1993). Models should occur in the simulated sample in proportion to their posterior probability. Integrating the posterior model probabilities for all models that include a given predictor variable yields the

conditional probability that the variable is a predictor. We performed Bayesian variable selection in WinBUGS.

We included geographic separation, dissimilarity of all plants, elevation, mean tree diameter, mean tree height, number of trees, and disturbance as candidate predictors of turnover of butterfly species. We included geographic separation, dissimilarity of riparian plants, elevation, wetted width, shade cover, water depth, water velocity (mean and maximum), substrate size, depth of detritus, vegetation depth, springbrook length, and disturbance as candidate predictors of turnover of aquatic macroinvertebrates. Variable selection was performed twice, with geographic separation included in the set of candidate predictors either as a single variable (distance between springs) or as geographic coordinates.

We performed variable selection with both linear models and cubic splines, with qualitatively similar results. We present only the posterior probabilities from the linear variable selection because these are more reliable due to Markov Chain Monte Carlo convergence difficulties for variables selection with spline models. The most probable models were re-fit with cubic splines and evaluated using DIC and pseudo- R^2 values.

Results

Spatial models

Turnover of butterfly species was related to geographic separation of springs: dissimilarity of species composition increased as distance between springs increased (Figure 1a). Both the linear model and the *I*-spline model were supported by the data (i.e., had lower DIC values than the null model). The relationship between species turnover and geographic separation, however, was relatively weak (Table 1).

We found little evidence that turnover of all aquatic macroinvertebrates was related to geographic separation; the null model had a lower DIC value than linear or *I*-spline spatial models (Table 2). For sedentary macroinvertebrates, the null model had the lowest DIC value. For the mobile species, the cubic spline model had the lowest DIC value, indicating a nonlinear relationship between species turnover and geographic separation.

For springs separated by < 20 km, the relationship between species turnover and geographic separation of springs was weak to nonexistent for both mobile and sedentary macroinvertebrates (Figure 1b, c). The effect of geographic separation was stronger at distances > 20 km, but the magnitude of effect was uncertain because all data points at these distances were associated with a single site, Willow Creek. Because Willow Creek was the only spring > 20 km from any other spring, it is impossible to gauge whether the dissimilarity of its aquatic fauna to species at the remaining springs was related directly to its geographic isolation. This uncertainty is included explicitly in the models via the site-specific error terms. The uncertainty also is reflected in the wide credible intervals about the fitted relationships and in the DIC value for the spatial model of turnover of

sedentary species, which was higher than the null model DIC (Table 2). When we ignored the interdependencies within the dissimilarity matrix and fitted models without site error terms, the fitted relationships had narrow credible intervals and spatial models for sedentary species had lower DIC values than corresponding null models. That is, if the interdependencies within the dissimilarity matrix were ignored we would be overconfident, given the true nature of the data, about the fitted relationship between species turnover and geographic separation. The spatial model for the mobile species had the same uncertainty, but evidence for a relationship with geographic separation was stronger because Willow Creek shared no mobile species with 11 of the 12 remaining springs and because there was some (albeit weak) evidence of a positive relationship between turnover and geographic separation among the remaining sites (i.e., the two springs that were nearest to each other shared the greatest number of mobile species).

Influence of plant assemblages

Species turnover of all plants was a better predictor of butterfly species turnover than geographic separation (Table 1) Dissimilarity of plant composition increased as geographic separation increased, so it was impossible to separate completely the effects of plant composition from the effects of geographic separation on butterfly species turnover. However, partial R_c^2 values showed that some variation in turnover of butterfly species was associated with plant turnover but not with geographic separation, whereas all of the variation in butterfly turnover that was associated with geographic separation also was associated with plant turnover.

There was little association between turnover of mobile aquatic macroinvertebrates and turnover of riparian plants. The I -spline model that included only turnover of riparian plants as a predictor of turnover of mobile macroinvertebrates had a marginally lower DIC value than the null model, but the R_c^2 value was low (Table 2).

Based on DIC values it appeared that species turnover of riparian plants was a better predictor of turnover of sedentary macroinvertebrates than geographic separation. The R_c^2 values appeared to contradict this inference (Table 2), but the relatively high R_c^2 for geographic separation was entirely driven by Willow Creek. If Willow Creek was excluded from the analysis then the association between turnover of sedentary macroinvertebrates and turnover of riparian plants, although weak, certainly was stronger than the association between turnover of sedentary macroinvertebrates and geographic separation. The systematic error associated with Willow Creek (ψ) was large in the model that included turnover of riparian plants. In part, this explains why the overall fit of the latter model was better than the spatial model: the systematic error accounts for variation in turnover of sedentary macroinvertebrates associated with turnover of riparian plants as well as an additional source of systematic variation associated with Willow Creek, which may or may not reflect an effect of geographic isolation.

Selection of variables

When Bayesian variable selection was applied to all potential predictors, elevation was selected as the most probable predictor of turnover of butterfly species, with a posterior probability of 1 (Table 3). All other variables had posterior probabilities lower than the prior probability of 0.22. Because the posterior probabilities are

conditional on the set of candidate predictors, a low probability does not necessarily mean that variation in the response variable is not associated with variation in a candidate predictor, only that the predictor variable has low probability of inclusion in the most parsimonious model. Hence geographic distance and turnover of all plant species were unlikely to be included in the best model when elevation was included as a predictor, but if elevation was not considered as a predictor then geographic distance and turnover of all plant species had high probabilities (0.78 and 0.81, respectively) of being included in the best model.

For the 17 springs for which data on both butterfly assemblages and plant assemblages were available, a relatively large proportion of the variation in turnover of butterfly species was associated with differences in elevation (Figure 2), including all of the variation that was associated with turnover of all plant species (i.e., partial R^2 for plant turnover = 0) and geographic separation (Table 1). When all 23 sites for which butterfly data were available were modelled, the proportion of variation associated with differences in elevation was lower, but still substantial.

Geographic distance or UTM coordinates were the only variables selected as predictors of turnover of mobile aquatic macroinvertebrates (Table 4).

Turnover of riparian plant species and geographic coordinates had some probability of being predictors of turnover of sedentary macroinvertebrates (Table 4). Examination of DIC and pseudo R^2 values of probable models fit with cubic splines suggested that turnover of riparian plants was a better predictor of turnover of sedentary macroinvertebrates even when Willow Creek (which drove any spatial pattern) was included in analyses.

Table 1. Deviance information criterion (DIC) and pseudo R^2 values for Generalized Dissimilarity Models (GDMs) relating turnover of butterfly species to environmental variables. The null model is a GDM with only an intercept and site-level random effects. R^2 values indicate the total proportion of variation in species turnover explained by the covariate and the site-level random effects. R_c^2 indicates the proportion of total variation explained by the covariate(s) component of the model only (see text). Partial R_c^2 values indicate the change in R_c^2 when a covariate is added to a model. *Because coefficients are positive (there is effectively zero probability of a coefficient having value exactly = 0 under a half-normal prior), the addition of covariates can reduce R_c^2 .

	DIC	DIC	R^2	R^2	R_c^2	R_c^2	partial R_c^2
# sites	23	17	23	17	23	17	17
null model	-414.6	-237.2	0.33	0.38			
geographic separation	-423.6	-237.7	0.37	0.40	0.07	0.16	-0.02*
dissimilarity of all plants		-256.4		0.47		0.25	0.07
geographic separation and plants		-249.66		0.46		0.23	
elevation	-454.7	-247.6	0.46	0.48	0.19	0.32	0.07
elevation and plants		-247.0		0.49		0.32	

Table 2. Deviance information criterion (DIC) and pseudo R^2 values for Generalized Dissimilarity Models relating butterfly species turnover to environmental variables.

		DIC	R^2	R_c^2	partial R_c^2
All aquatic macroinvertebrates	null model	-174.7			
	geographic separation	-171.1	0.67	0.21	0.15
	dissimilarity of riparian plants	-175.2	0.71	0.15	0.09
	geographic separation and riparian plants	-171.4	0.70	0.30	
Mobile macroinvertebrates	null	-216.7	0.59		
	geographic separation	-219.5	0.59	0.43	0.40
	dissimilarity of riparian plants	-217.8	0.60	0.04	0.01
	geographic separation and riparian plants	-214.2	0.60	0.44	
Sedentary macroinvertebrates	null	-164.5	0.65		
	geographic separation	-162.6	0.65	0.16	0.11
	dissimilarity of riparian plants	-165.3	0.68	0.12	0.07
	geographic separation and riparian plants	-162.2	0.67	0.23	

Table 3. Posterior probabilities that each environmental variable was a predictor (conditional on the set of candidate predictors) of turnover of butterfly species.

	probability	probability
geographic distance		0.002
dissimilarity of all plants	0.001	0.001
longitude	0.084	
latitude	0.113	
elevation	1	1
mean tree diameter	0	0.001
mean tree height	0.006	0.004
number of trees	0.002	0
disturbance	0.001	0.001

Table 4. Posterior probabilities that each environmental variable was a predictor
(conditional on the set of candidate predictors) of turnover of aquatic macroinvertebrates.

	sedentary	sedentary	mobile	mobile
distance between springs		0.094		0.444
longitude	0.532		0.772	
latitude	0.513		0.687	
dissimilarity of riparian plants	0.333	0.467	0.012	0.023
elevation	0.011	0.036	0.009	0.019
wetted width	0.09	0.235	0.007	0.023
shade cover	0.002	0.001	0.007	0.011
water depth	0.061	0.079	0.011	0.02
water velocity (mean)	0.006	0.007	0.049	0.096
water velocity (maximum)	0.005	0.003	0.073	0.107
substrate size	0.018	0.015	0.007	0.01
depth of detritus	0.004	0.009	0.022	0.033
vegetation depth	0.102	0.193	0.032	0.061
springbrook length	0.001	0.007	0.026	0.056
disturbance	0.002	0.006	0.004	0.006

Figure 1. Relationships between species turnover and distance between springs for (a) butterflies, (b) mobile aquatic macroinvertebrates, and (c) sedentary aquatic macroinvertebrates. Fitted lines show relationships with 95% credible intervals.

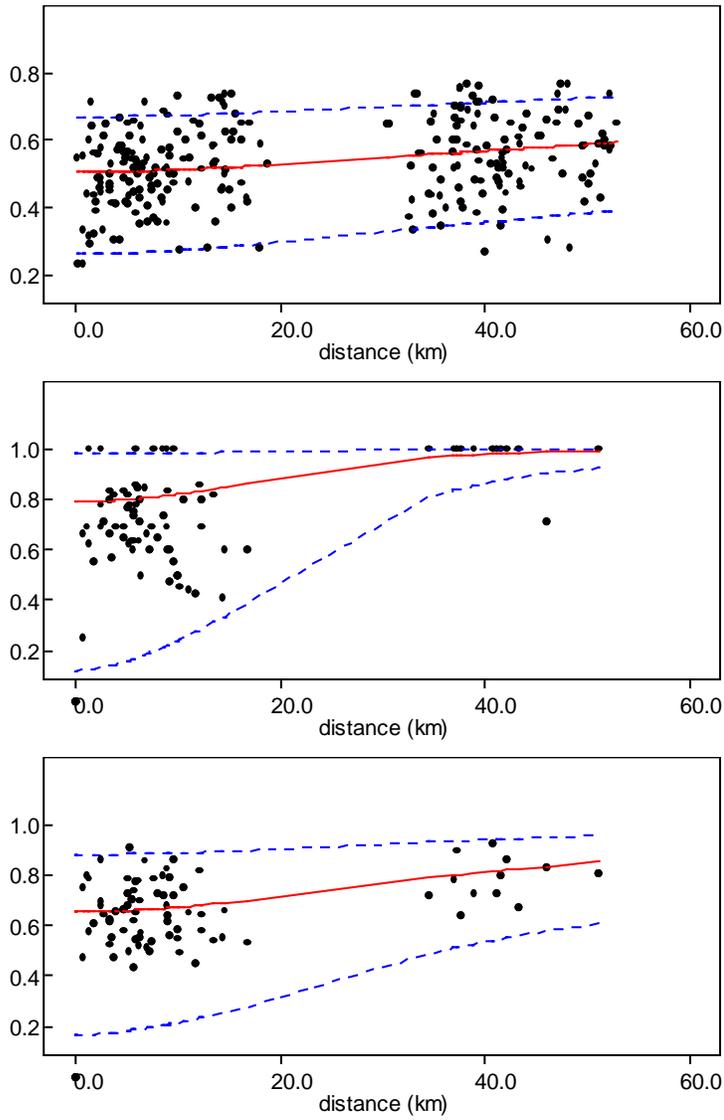


Figure 2. Relationship between turnover of butterfly species and elevation. (a) Turnover of butterfly species versus difference in elevation, with posterior means and 95% credible intervals of fitted values. (b) Fitted monotonic transformation of elevation, suggesting that a given change in elevation had greater effect on species turnover at high elevations than at low elevations.

