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Ecological Applications, Vol. 2, No. 4. (Nov., 1992), pp. 404-410.

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EFFECT OF THE FOCAL TAXON ON THE SELECTION OF NATURE RESERVES¹

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Abstract. Among the numerous site-ranking or reserve selection approaches is to select reserves based on the current distribution of a suite of species. This approach only requires distribution data for the species in the "focal taxon." To what extent is the proposed reserve network dependent on the species included in the focal taxon? Can a suite of species act as an umbrella or indicator for other species whose distribution was not directly considered?

A simple reserve selection algorithm was applied to species lists from sites where multiple taxa were sampled. The algorithm selected sites so that each species in the focal taxon was represented in at least one reserve. The species lists were compiled for birds, mammals, reptiles, and plants on islands in the Gulf of California, and for birds, mammals, and plants in canyons in San Diego County, California. Within both data sets, there were significant rank correlations ($P < .01$) between the number of species in different taxa per potential reserve. Yet the number of proposed reserves that satisfied the selection algorithm differed strongly between taxa. For example, 2 of 25 canyons were in the San Diego bird reserve network, but 10 of 25 canyons were in the native plant reserve network. The area of the proposed reserves selected by the algorithm ranged from a minimum of 3.2% of the total area for San Diego bird reserves to a maximum of 98.3% of the total area for the Gulf of California plant reserves. The bird reserves included only 45-78% of the species in the other taxa. Conversely, the plant reserve network would contain 88-100% of the vertebrate species. Thus, plants were better indicators than birds for reserve establishment. Plant occurrences were less ordered than bird occurrences, and there were 10 or 20 times more plant species than bird species. The better umbrella taxon was more speciose or had less pattern to species occurrences. Rather than a literal application of plants as reserve indicators, a better approach would be to collect some preliminary distribution data for a number of taxa in the potential reserve network and use these preliminary data to define the focal taxon (or taxa).

Key words: *biodiversity; California; decision-making algorithm; indicator species; nature reserves; nested subsets.*

INTRODUCTION

The process of selecting sites for a nature reserve network is a part of the process of reserve design and management. This paper considers a simple reserve selection algorithm, which is based on the method described by Margules et al. (1988). The algorithm selects sites so that each species within a focal taxon is represented in at least one reserve. The algorithm, or decision rule, is applied to a presence-absence matrix for a focal taxon. Thus species in the focal taxon are treated equally.

I will not consider issues that are generic to reserve design and selection. Others have developed extinction models, or considered the importance of perimeter-area ratios to species persistence. For example, increased extinction risk of small populations or the detrimental effects of inbreeding have been used as design constraints (Boecklen 1986, Goodman 1987, Schaffer 1990). The shape of a reserve may affect its manage-

ment as well as the extinction risk of its residents (Schonewald-Cox and Bayless 1986, Buechner 1987). There have been many applications of island biogeographic theory to nature reserve design (Diamond 1975, Gilpin and Diamond 1980). The biogeographic approach has resulted in the SLOSS (single large or several small reserve) debate.

The purpose of this paper is to see whether species in a focal taxon can act as biodiversity umbrellas; selecting reserves that include all species in the focal taxon also includes species in other taxa. Plants and birds have been used to select reserve networks (Götmark et al. 1986, Rebelo and Siegfried 1990). For example, Rebelo and Siegfried (1990) used the number of Proteaceae species to select reserves in the South African Fynbos. I tested the ability of plants or birds to act as an umbrella taxon for two sets of published distribution data (species lists). Both data bases included distribution data for plants, birds, and mammals, and one data base also included reptiles. These data were subjected to a simple version of Margules' et al. (1988) reserve selection algorithm.

¹ Manuscript received 22 August 1991; revised 26 January 1992; accepted 28 January 1992.

If taxa differ in their utility as reserve selection indicators, then what factors cause this difference and can these factors be used to choose an umbrella taxon a priori? The factor must summarize some aspect of an entire presence-absence matrix (or a set of species lists for potential reserves). The number of species may be a useful statistic since it can be estimated from a collector's curve before the complete distribution data are gathered. Another possible measure of a taxon's utility as an umbrella taxon is the orderedness statistic (Ryti and Gilpin 1987). Orderedness of species occurrences is related to the concept of nested subsets (Patterson and Atmar 1986). Perfect nestedness (or perfect orderedness) implies that the more-narrowly distributed species occur at a subset of sites where more broadly distributed species occur. A perfectly ordered archipelago would need only a single site to include all species.

METHODS

The reserve selection algorithm, or decision rule, employed in this paper was a simple version of the numerical algorithm used by Margules et al. (1988). The basic goal was to represent each species at least once in the list of proposed reserves. The selection algorithm was applied to a presence-absence matrix for s species at i sites. Let $a_{jk} = 1$, if the j th species occurred at the k th site. The algorithm was dependent on two quantities: the number of species at site k (S_k) and the number of sites where species j was found (I_j). The algorithm consisted of the following steps:

- 1) Sort species by the number of occurrences (I_j); thus, $I_1 = I_{\min}$ and $I_s = I_{\max}$.
- 2) Test the value of I_j for each species $j = 1$ to s :
 - a) If $I_j = 1$, then include the site where species j is found in the list of proposed reserves and increment j ($j \rightarrow j + 1$);
 - b) If $I_j \geq 2$ and species j already occurs in a proposed reserve, then increment the species counter ($j \rightarrow j + 1$);
 - c) If $I_j \geq 2$ and species j was not in a proposed reserve, then mark the site with the greatest richness (number of species) as a proposed reserve and increment the species counter ($j \rightarrow j + 1$). Select site k where $S_k = \text{maximum}(S_k | a_{jn} = 1)$.

The reserve network was defined as the list of proposed reserves that included at least one occurrence of each species. Two examples show how the reserve network was produced. In the first example (Table 1a), site E contained all of the species and was the one reserve selected. In the second example (Table 1b), three sites (B, D, and E) were needed to include all of the species.

This algorithm was order-dependent. When there was a tie between sites at step 2c (equal number of species), then the first site in the list was added to the

TABLE 1. Hypothetical presence-absence matrices, where sites are listed by columns and rows represent species. (a) In this perfectly ordered matrix (orderedness = 100%), only site E is needed to select all species. (b) In this partly ordered matrix (orderedness = 18%), sites B, D, and E are needed to select all species.

| Species, j | Site | | | | | No. occurrences, I_j |
|-----------------------------|------|---|---|---|---|------------------------|
| | A | B | C | D | E | |
| a) Perfectly ordered matrix | | | | | | |
| 1 | 0 | 0 | 0 | 0 | 1 | 1 |
| 2 | 0 | 0 | 0 | 0 | 1 | 1 |
| 3 | 0 | 0 | 0 | 1 | 1 | 2 |
| 4 | 0 | 0 | 0 | 1 | 1 | 2 |
| 5 | 0 | 0 | 1 | 1 | 1 | 3 |
| 6 | 0 | 0 | 1 | 1 | 1 | 3 |
| b) Partly ordered matrix | | | | | | |
| 1 | 0 | 0 | 0 | 0 | 1 | 1 |
| 2 | 0 | 0 | 0 | 1 | 0 | 1 |
| 3 | 0 | 1 | 0 | 1 | 0 | 2 |
| 4 | 0 | 0 | 0 | 1 | 1 | 2 |
| 5 | 1 | 1 | 1 | 0 | 0 | 3 |
| 6 | 0 | 1 | 1 | 0 | 1 | 3 |

list of proposed reserves. Since sites were ordered by area, from the largest to the smallest, the largest-area site was added to the list of reserves. The importance of ties to reserve selection and other possible tie-breaking protocols are discussed below.

The performance of this selection algorithm was assessed in two different ways. First, determine whether the list of proposed reserves were taxa-dependent. Second, determine the importance of narrowly distributed species to reserve selection. For example, the reserve network for species that occur at a single site (step 2a) may include all of the more broadly distributed species.

The selection algorithm was applied to two sets of species lists. The first data set was the list of land birds, plants, reptiles, and mammals on 18 islands in the Gulf of California (Cody 1983, Cody et al. 1983, Murphy 1983, Lawlor 1983). Varieties and subspecies were not considered separately. The islands were: Tiburón, Angel de la Guarda, San Esteban, San Lorenzo Sur, San Marcos, San Lorenzo Norte, Salsipuedes, San José, Cerralvo, Carmen, Espiritu Santo, Santa Catalina, Santa Cruz, Monserrate, Coronados, Danzante, San Francisco, and San Diego (but note: no plant data were reported for San Lorenzo Norte). The frequency distribution of island area was negatively skewed; the two largest islands comprised 72% of the total island area. The islands also covered a wide latitudinal range, where 800 km separated the most northern from the most southern island. Islands have been separated from the mainland for at least 10 000 yr. The second data set was the list of birds, plants, and mammals in canyons (habitat islands) in San Diego County, California (Soulé et al. 1988, D. Bolger, unpublished data). The canyons were fragments of native chaparral that have been isolated due to urban development in San Diego. The

TABLE 2. Summary of the number of reserves and the proportion of the area required to include all of the birds, mammals, reptiles, or plants. (a) Data from 18 islands in the Gulf of California. (b) Data from 25 canyons (habitat islands) in San Diego County (percentage of area is calculated from the chaparral area in each canyon).

| Taxon | Number of reserves | % of area in network* | Number of species | Prop. 1's† | Orderedness (%)‡ |
|------------------------|--------------------|-----------------------|-------------------|------------|------------------|
| a) Gulf islands | | | | | |
| Birds | 3 | 51.4 | 29 | 0.467 | 68.7 |
| Mammals | 7 | 64.2 | 23 | 0.113 | 33.5 |
| Reptiles | 12 | 98.2 | 73 | 0.157 | 29.2 |
| Plants | 13 | 98.3 | 533 | 0.208 | 37.8 |
| All taxa | 15 | 99.7 | 658 | 0.209 | 38.9 |
| b) San Diego canyons | | | | | |
| Birds | 2 | 3.2 | 8 | 0.425 | 81.2 |
| Rodents and Lagomorphs | 2 | 30.9 | 11 | 0.324 | 51.9 |
| Mammals§ | 3 | 34.0 | 17 | 0.395 | 53.8 |
| Plants | 10 | 66.1 | 87 | 0.341 | 44.4 |
| All taxa | 8 | 62.5 | 112 | 0.355 | 44.0 |

* Total area of the Gulf islands = 2919 km²; total area of the San Diego canyons = 377 ha.

† The proportion of 1's is an estimate of the probability of finding a species at a site.

‡ Orderedness indicates the degree that species occurrences follow a nested pattern. (100% orderedness is a perfectly nested pattern.)

§ All species.

canyons used in the analyses in this paper were numbered 1–6, 8, 10–12, 14–17, 21–24, 26–29, 34, 36, 37 in Soulé et al. (1988). This subset of canyons was sampled for birds, plants, and mammals. The canyons represented a much smaller spatial scale (about 50 km between the most distant sites), and more recent time since fragmentation (10–100 yr).

The orderedness of species occurrences was determined by the technique described by Ryti and Gilpin (1987). This analysis yielded a single measure of nestedness. This measure, orderedness, was the explained variance of a logistic model of the presence-absence matrix. A perfectly nested occurrence pattern corresponds to 100% orderedness (Table 1a). While some non-random patterns (e.g., a checkerboard) are not ordered, orderedness is a measure of how randomly species are distributed. Orderedness typically ranges between 20 and 80% (Ryti and Gilpin 1987), where lower values of the orderedness statistic correspond to more-random occurrence patterns. The other presence-absence matrix example (Table 1b) had 18% orderedness. A perfectly ordered archipelago will only require a single reserve, typically the largest, to include all of its species.

RESULTS

The reserve networks that resulted from the selection algorithm are summarized in Table 2. To include all eight bird species found in the San Diego canyons, only two canyons, which comprised 3.2% of the total chaparral area, were selected as reserves. However, to include all 87 native plant species found in the San Diego canyons, 10 canyons were included in the reserve network (66.1% of the total chaparral area). For either data set, the number of sites (or proportion of the total area) in the reserve network was least for birds and

greatest for plants. Mammals and reptiles required less extensive reserve networks than plants, but were much larger in area or number than birds.

The taxa required different numbers of sites in the proposed network, even though there were significant correlations in species number ($P < .01$). The magnitude of these correlations was from 0.7 to 0.85 for the Gulf taxa and from 0.5 to 0.8 for the San Diego taxa. For example, Gulf bird richness (number of species) was strongly correlated with plant richness ($r = 0.769$, $n = 17$, $P < .01$), but the bird reserve network contained 3 islands and the plant reserve network was composed of 13 islands.

There were also differences between the data bases. The proportion of the total island area in the Baja reserve network for birds, mammals, or plants was greater than the proportion of the total canyon area in the San Diego reserve network (Table 2). There were more single-island endemics on the Baja islands than in the San Diego canyons (Table 3). Nineteen of 112 species (17%) were restricted to a single canyon, but 281 of 658 species (43%) were on a single island.

The proportion of the total area in the reserve network (relative reserve area) was correlated with the orderedness of the taxa ($r = 0.85$, $n = 7$, $P < .01$; rodents-lagomorphs were not considered separately from mammals), and with the taxon richness (log of the number of species; $r = 0.88$, $n = 7$, $P < .005$). Plants were the most diverse (78 or 81% of the total species) and least ordered of all the taxa, and also required the most extensive reserve network (Table 2). The proportion of 1's was positively correlated with orderedness ($r = 0.89$, $n = 7$, $P < .005$). This pattern was also noted by Ryti and Gilpin (1987). The proportion of 1's was an estimate of the average probability that a species occurred at a site. Thus the pro-

portion of 1's indicated how broadly species were distributed over sites, or the overall colonizing success of a taxon. More-narrowly distributed (and less vagile) taxa tended to be more randomly distributed across sites.

The decision rule performed differently for the island data as compared to the canyon data. Almost all of the Gulf of California reserves were defined by the rare species (species observed on a single island) (Table 3a). Species restricted to a single canyon were not as important in the San Diego canyon data (Table 3b). For example, all 13 reserves were defined by the 224 plant species that occurred on a single island, but only 7 of 10 canyons were defined by the 17 native plant species that occurred in a single canyon (Table 3).

Only 45–78% of the other taxa were included in the bird reserve network (Table 4). One hundred seventy-four species were missing from the Gulf of California bird reserve network, and 53 species were absent from the San Diego bird reserve network. Nearly all of the the vertebrates were included in the plant reserve network (Table 5). Thus, the vertebrate reserve networks were mostly a subset of the plant reserve network. Only two reptile species in the Gulf of California and one bird species in the San Diego canyons (the Cactus Wren) were missing from the plant reserve networks.

DISCUSSION

Three important caveats apply to this simplified reserve-selection process. First, the reserve selection algorithm should be used in conjunction with other design and management criteria. For example, a stochastic extinction model could be used to define a critical population size and minimum reserve area. Second, only species that require special protection should be included in the focal taxon. One may exclude species that

TABLE 3. Decision rule evaluation. This table lists the number of reserves selected after considering species that occurred at only one site (i.e., where $I_i = 1$). (a) Data from 18 islands in the Gulf of California. (b) Data from 25 canyons in San Diego County.

| Taxon | Number of species where $I_i = 1$ | Number of reserves selected | Number of species in reserve network |
|------------------------|-----------------------------------|-----------------------------|--------------------------------------|
| a) Gulf islands | | | |
| Birds | 7 | 2 | 28 |
| Mammals | 14 | 7 | 23 |
| Reptiles | 36 | 10 | 70 |
| Plants | 224 | 13 | 533 |
| b) San Diego canyons | | | |
| Birds | 1 | 1 | 2 |
| Rodents and Lagomorphs | 0 | 0 | 0 |
| Mammals* | 1 | 1 | 11 |
| Plants | 17 | 7 | 84 |

* All species.

TABLE 4. Effect of using the bird reserve network on the number of species in other taxa included in the reserve network. (a) Gulf of California islands, 72% of all other taxa are included in three bird reserves. (b) San Diego County canyons, 49% of all other taxa are included in the two bird reserves.

| Taxon | Number of species in bird reserve network | % of total species in taxon |
|------------------------|---|-----------------------------|
| a) Gulf islands | | |
| Birds | 29 | 100 |
| Mammals | 18 | 78.3 |
| Reptiles | 45 | 61.6 |
| Plants | 392 | 73.5 |
| b) San Diego canyons | | |
| Birds | 8 | 100 |
| Rodents and Lagomorphs | 6 | 54.6 |
| Mammals* | 12 | 70.6 |
| Plants | 39 | 44.8 |

* All species.

are common in human-disturbed habitats. Third, species distribution data are assumed to be completely accurate; each species occurs only at sites indicated by the published species lists.

The long-term viability of populations within the reserve network can be addressed by population viability analysis (Gilpin and Soulé 1986). Detailed demographic, genetic, and distributional data would be needed to complete a population viability assessment for each species. For example, a detailed metapopulation model could be used to define reserve locations for a single species or a set of species. Economic and land-use issues should also be a part of the reserve design and selection process (Grumbine 1990). The data requirements of the best approach are overwhelm-

TABLE 5. Effect of using the plant reserve network on the number of vertebrates included in the reserve network. (a) Gulf of California islands, 98% of the vertebrates are included in 13 plant reserves. (b) San Diego County canyons, 96% of the vertebrates are included in the 10 plant reserves.

| Taxon | Number of species in plant reserve network | % of total species in taxon |
|------------------------|--|-----------------------------|
| a) Gulf islands | | |
| Birds | 29 | 100 |
| Mammals | 23 | 100 |
| Reptiles | 71 | 97.3 |
| Plants | 533 | 100 |
| b) San Diego canyons | | |
| Birds | 7 | 87.5 |
| Rodents and Lagomorphs | 11 | 100 |
| Mammals* | 17 | 100 |
| Plants | 87 | 100 |

* All species.

ing—roughly 20 yr of demographic data as well as the impacts of various active and passive management strategies on species survival. It is an open question whether data of appropriate quality can be supplied to decision-makers in time to establish a reserve network. It is not surprising that abbreviated ranking systems for natural areas have been developed. The approach described by Margules et al. (1988) and applied here is one possible ranking system. The Nature Conservancy's "element-based" approach uses professional judgment and objective information to rank sites by their rarity and vulnerability (Duever and Noss 1990). Another ranking system, based on a cladistical analysis, was recently proposed by Vane-Wright et al. (1991). The cladistic method ranks sites by their taxonomic diversity, where the goal is to preserve hot spots of evolutionary-scale diversity. With a variety of site-ranking or reserve-selection methods available, it is encouraging that one study reported that two methods (economic and population viability) gave similar results (Ayres et al. 1991).

Any decision rule used in environmental planning should be subjected to a formal sensitivity analysis. This analysis would enter test data, as was done in this paper, to see if the resulting decision (reserve network) is within expectations. Random reshuffling of the data can test the impact of initial conditions on the algorithm (see Margules et al. 1988). Another part of the sensitivity analysis would explore alternate decision rules. For the decision rule explored in this paper use another tie-breaking procedure. The tie-breaking step selected among two (or more) candidate reserves that have the same number of species. In the present case the algorithm selected the larger site to be included in the reserve network, but it is equally logical to select the smaller of the two sites for the reserve network. This tie-breaking procedure was not important for the occurrence data examined; most of the reserve network was selected during the first step in the algorithm (step 2a, select sites where single-occurrence species are found).

The application of a simple reserve-selection algorithm to plant and vertebrate occurrence data showed that plants did act as an umbrella for the vertebrates, but birds were a poor umbrella taxon. Specifically, the reserve networks based on plants as the focal taxon included >96% of the vertebrates, but the reserve networks based on birds as the focal taxon only included 49–72% of the other taxa. The plants were both more diverse and less ordered than birds. Previous analysis of occurrence data for a variety of taxa showed that the orderedness statistic was related to the vagility of the taxon; bird occurrences were most ordered and other vertebrates and plants were less ordered (Ryti and Gilpin 1987).

No single taxon will be completely effective as a reserve selection indicator. While plants were the better umbrella taxon, we should be careful in extrapolating

from a sample of two systems to other cases. As noted above, three vertebrate species were missing from the plant reserve networks, and from these data I cannot predict how well a plant reserve network will include invertebrates. The most prudent approach will be to collect distribution data for all species before a focal taxon is chosen. One use of these preliminary data would be to compute the orderedness of the taxa or estimate the total number of species. This information could be used to define the focal taxon (least ordered or most diverse). The most direct method would apply the selection algorithm to these preliminary data, and see which taxon, if any, adequately includes other species.

The Gulf reserve networks were defined more frequently by narrowly distributed species than were the San Diego canyon reserve networks. This difference was related to the greater frequency of narrowly distributed species in the Gulf taxa as compared to the San Diego taxa (43% vs. 17%). One possible explanation was that the San Diego canyons have not reached equilibrium (Bolger et al. 1991), and that further extinctions will increase the number of narrowly distributed species.

Another result of practical importance was the size of the reserves selected. Never did a single site include all species in a taxon, as would be adequate for a perfectly nested taxon. Both large and small sites were selected, which included the largest sites plus some smaller sites. It is obvious that area per se cannot be used as a sole indicator for reserve selection, although some measure of habitat structure or habitat heterogeneity may be helpful (Usher 1991).

A smaller proportion of the total area was in the reserve network for the habitat islands compared to the true islands (compare Table 2a and 2b). This difference was probably related to the size of the system and the age since isolation. The Gulf of California islands have had enough time for endemics to evolve and for species to go extinct. There have been some extinctions in the canyons of birds over decades of fragmentation (Bolger et al. 1991), but equilibrium has probably not been reached. Caution should be advised in applying a minimal reserve selection to an initially continuous habitat, since some species will go extinct due to habitat fragmentation.

With one exception, a large proportion of the total area was in the reserve network. Excluding the San Diego birds (3% of the total area in the bird reserve), these proportions ranged from 30% to 99% for the taxa considered in this paper, and values between 6% and 45% have been reported in the literature (Margules et al. 1988, Pressey and Nichols 1989, Rebelo and Siegfried 1990). It may not be possible to set aside all the sites needed, and some ranking of the "conservation value" of species must be made. These rankings can be made in an ad hoc fashion, or else based on some theoretical arguments of extinction vulnerability. For

species that are already rare, the distinction between these methods is not important, since the data used to drive the extinction models cannot be precisely measured. For example, an estimate of population size is used to estimate the population growth rate (Dennis et al. 1991), which may increase the size of the confidence limits on mean extinction time. One rational approach would be to only consider narrowly distributed species. The approach taken in this paper automatically attaches greater weight to endemic species or species that occur at a single site. Unfortunately, the narrowly distributed species selected most of the sites (and area) for the plant reserve networks (see Table 3), and thus do not exclude many sites from the reserve network.

A larger question is how species lists will be used (when they are available) with other selection constraints. For example, reserve edges and their management affect the animals in the reserve (Schonewald-Cox and Bayless 1986). Operational constraints must be considered, both in species richness sampling and in the selection of reserve networks. Frequently, reserve planners may be limited to sub-optimal areas based on restricted land availability (Rebello and Siegfried 1990).

An important shortcoming of the approach taken in this paper is the lack of any predictions of extinctions. Extinctions may be greatest for reserves created from previously continuous habitat. There is evidence for rapid extinctions of the chaparral requiring birds in the San Diego canyons due to habitat fragmentation (Bolger et al. 1991). Some researchers have used land-bridge islands to estimate extinction rates (Richman et al. 1988), but truly conclusive data on the relationship between fragmentation and extinction requires large-scale experiments (for example, Lovejoy et al. 1984). One practical solution is to select reserves so that each species occurs at least two or three times, where populations that go extinct may be rescued by populations on neighboring reserves (Hanski 1989). An analysis that determines the number of "replicate" reserves per species should consider both beneficial (less susceptible to local catastrophes) and detrimental effects (greater management costs) of larger numbers of reserves.

A shortcoming of any reserve selection process is that it is based on current climatic conditions. While there is much agreement on the likelihood of global warming, the effects of climate change on specific sites cannot be predicted with great accuracy. One solution is to include potential refugia within the reserve network, as suggested by Rebello and Siegfried (1990) for South African Fynbos.

In conclusion, the results suggest that an empirical approach to reserve design and selection should be used. Objective ranking of the extinction vulnerability of species should be used to define a list of target species. Then preliminary distribution data should be collected and analyzed to see if an umbrella taxon or species can be defined. In cases where no umbrella

species can be defined, then use the entire list of target species to select the sites where the occurrences within the target group are maximized.

ACKNOWLEDGMENTS

I thank D. Bolger, D. Debinski, M. Gilpin, D. Goodman, B. Patterson, J. Pickett, W. Swanson, B. Taylor, and two anonymous reviewers for their comments on previous versions of the manuscript. I also thank D. Bolger for sharing unpublished mammal and plant data from the San Diego Canyon Project.

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