Coarse-Scale Gradient Analysis of Environmental Factors in Relation to Plant Species Diversity for Vegetation Communities of California

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Abstract

Plant species data from floristic subregions for chaparral, coastal sage scrub, foothill woodland, and yellow pine forest communities in California were analyzed for species turn-over in relation to environmental variables. Species-community data were related to climate and topography using detrended canonical analysis (DCA) and canonical correspondence analysis (CCA), to identify factors associated with composition gradients. Total species-community variance explained by the first two DCA/CCA axes was 65/59% for chaparral, 61/57% for coastal sage scrub, 49/43% for foothill woodland, and 60/48% for yellow pine forest. Seasonal variability and climatic extremes contributed more to species variation than mean annual climatic conditions. Species gradients were more strongly associated with climatic conditions during the growing season than in winter. Results for these vegetation communities confirm previous fine-scale studies, supporting the notion that local community structure is the result of both regional and landscape processes. Analysis of coarse-scale historical floral data reduced problems with spatial and temporal sampling effects found in many fine-scale field studies.

I. INTRODUCTION

The identification of factors controlling the distribution, abundance, and diversity of species in communities continues to be a central problem in community ecology, and is becoming more important for ecosystem vulnerability studies Peters and Lovejoy [35]. Community structure is considered a product not only of local physical conditions and interactions among species, but also of regional climatic constraints, and of historical processes such as dispersal and speciation, migrations, and extinction (Neilson and Wullstein [30], Ricklefs [40], Menge and Olson [27]). Plant community ecologists have devoted considerable effort to quantifying local- to landscape-scale variation in vegetation. Factors associated with fine-grained patterns of community composition often are well known, but differ among localities. However, few quantitative, coarse-scale descriptions provide context for landscape differences (but see Denton and Barnes [8], Ohmann and Spies [32], Qi and Yang [38]), while the synthesis and collation of plant community data for regional analysis has been cited as a major research need (Franklin [11]). The capability of deriving robust relationships between coarse-scale environmental measures and terrestrial properties, like floristic richness and composition, can facilitate prioritization in the monitoring of those variables af-

fecting landscape level diversity.

Most quantitative studies of vegetation communities have been limited to incomplete segments of regional environmental gradients and generally have been conducted at fine scales (e.g., Curtis and McIntosh [5], Whittaker and Niering [55], del Moral and Watson [7], Westman [51], Allen and Peet [1], Allen et al. [2], Parker [34]). Some regional- and continental-scale studies have quantified patterns of species diversity (e.g., Glenn-Lewin [12], Richerson and Lum [39], Currie and Paquin [4], Qi and Yang [38]), but have not evaluated species-environment gradients within a community. Ohmann and Spies [32], however, synthesized a large number of fine-scale field plots in the woody vegetation communities across Oregon and quantitatively related the species plot variation to coarse-scale environmental factors.

Scaling up from fine-scale ecological observations can create serious modeling problems (Levin [24]), as some ecological processes are non-stationary at coarser scales (Hengeveld [19]). Of importance is the realization that applied disciplines, such as conservation biology, remain focused at fine-scale issues, yet their methods are not easily extrapolated to address global ecological problems (Root and Schneider [41]). Geographic models of community composition and biological diversity should not only be based on fine-scale

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studies, but also include coarse-scale biological surveys. However, an understanding of the scale changes and interpretation from specific spatial analysis methods will be required.

Regional Species Composition in Relation to Environmental Factors and Scale

Whittaker [54] defined the landscape differentiation diversity concept for a given community as delta diversity, a change in species composition within a community type along climatic gradients or between geographic areas. In this study, we have hypothesized that macroclimate (coarse-scale temperature and moisture) is the primary associate of coarse-scale patterns of community composition, and that substrate and local factors (microclimate and landscape disturbance) are secondary. Macroclimate is thought to influence communities directly through physiological effects on organisms and by limiting populations (Woodward [56]). Macroclimate indirectly influences communities by modifying or regulating the importance of fine-scale factors and by favoring certain species and growth forms in interspecific competition (Woodward [56]). Studies have consistently demonstrated the primary importance of temperature and moisture (e.g., Kirkpatrick and Hutchinson [22], Westman [51], Allen and Peet [1], Allen et al. [2], Parker [34]). However, many of these studies did not distinguish the effects of macroclimate from microclimate, or they considered broad-scale climate only indirectly by observing vegetation change along complex fine-scale field plot gradients of elevation or latitude (Ohmann and Spies [32]).

Patterns of floristic composition have been associated in fine-scale gradient studies with elevation and through the stratification of large areas based on geological substrate and soil attributes (e.g., Whittaker [53], Waring and Major [48], Whittaker and Niering [55], Harrison et al. [17], Westman [51], Allen and Peet [1], Allen et al. [2]). For some communities, the interactions of disturbance, successional processes, and other environmental factors can determine the pattern of species composition locally (e.g., Westman [49], Zedler et al. [57], O'Leary and Westman [31]), but these are difficult to quantify in regional gradient studies based on fine-scale analysis.

Temporal and spatial scales of sampling vegetation can alter the interpretation of pattern and processes for a community. Whatever the mechanism, one's perception of a system and its fluctuations depends on the scale of observation. The utility of fine-scale field plots for regional gradient analysis is questionable for diverse and disturbance-adapted vegetation communities. For example, the Californian chaparral plant community has high species diversity, but this diversity can only be examined after proceeding through the entire successional process after fire disturbance (Vogl [47]). The benefits of a biological atlas of species distribution data derived from a long sampling time frame and at a coarse-scale would be to contain all those species that are found in a particular plant community throughout its entire successional cycle. This would allow the entire species diversity of a plant community to be examined at a large extent, but mask the fine-scale spatial heterogeneity of a community in a particular area. Therefore, the variability in species composition would not be underrepresented, as with the limited spatial and temporal extent of fine-scale field plot data, while macro-environmental relationships can also be examined with the appropriate coarse scaled species-community distribution data.

This paper examines the coarse-scale nature of plant species turnover in vegetation communities in relation to environmental gradients. Our primary objectives were to quantify environmental factors associated with regional gradients in the species composition of selected vegetation communities and to evaluate the coarse-scale results with known fine-scale results, in order to critically examine the role and utility of coarse-scale species data analysis for land characterization efforts. We have limited ourselves to four vegetation communities that are important conservation in the state of California: chaparral, coastal sage scrub, foothill woodland, and yellow pine forest.

II. DATA AND METHODS

A map of natural vegetation for California is provided by the CALVEG map (Matyas and Parker [26]), which depicts the distribution of 72 vegetation classes. These vegetation classes were reclassified to coarser vegetation communities of chaparral, coastal sage scrub, foothill woodland, and yellow pine forest as defined by indicator species in Munz and Keck [29]. The distributions of these four vegetation communities across California are presented in Figure 1.

Species distributions for vascular plants of California were taken from the Lum floristic database (Lum [25], Richerson and Lum [39]), as generated from the Munz and Keck [29] floristic catalog and supplemented with other data sources. This database identifies the probable presence-absence of species within the 94 floristic subregions of California (Figure 1). The membership of each species to one of the four specific vegetation communities was also encoded, as described by Munz and Keck [29]. Table 1 presents each plant community examined, its total species richness and the number of subregions it covers.

Figure 1. The California study area showing the overlay of the distributions of the four plant communities and the Lum subregions.

Table 1. Number of subregions that contain a portion of each plant community and the total number of species found in each plant community.

Community	Subregions	Species
Chaparral	60	840
Coastal Sage Scrub	19	558
Foothill Woodland	58	848
Yellow Pine Forest	56	1478

Environmental data were compiled in a raster GIS using a 1 km² grid and the Lambert Azimuthal Equal Area projection. The environmental data sets used for this study included a digital elevation model (DEM) produced by the U.S. Geological Survey, percent slope derived from the DEM, and a simplistic metric reflecting the radiation budget, called the northness index (sin[slope] * cos[aspect], Davis and Goetz [6]). Climatic data for the state was obtained from ZedX Inc. [58], providing interpolated monthly values of mean precipitation, minimum temperature, and maximum temperatures on a 1 km² grid.

The monthly climate data were reduced to a meaningful subset based on limiting factors. The selected climate variables for temperature included the maximum summer monthly temperature, the minimum winter monthly temperature, the mean annual temperature, and a seasonality index created by subtracting the maximum monthly temperature of January from July. Precipitation variables included the mean annual precipitation and a seasonality index based on the difference between the February and June monthly means. The selection of months used in the seasonal indices was supported by an assessment of the eigenvalues derived from a principal components analysis (PCA) on the climate datasets.

In order to relate the environmental data to the species database, the map of the four vegetation communities, derived from the CALVEG map, was intersected with the map of the 94 floristic subregions. This resulted in a map identifying the geographic distribution of the four vegetation communities within the 94 floristic subregions. The environmental datasets were then overlaid with the vegetation community-subregion map to calculate the mean, maximum, minimum, and standard deviation of each environmental variable for each community within a subregion.

The CANOCO program (ter Braak [45]) was used to conduct all gradient analyses. The dominant floristic trends for each community were determined based on the first two axes of an indirect gradient analysis by detrended correspondence analysis (DCA). Eigenvalues, biplots, and canonical trend surface maps derived from DCA were used to elucidate the magnitude and spatial configuration of gradients in species composition for each community. Pearson correlation analysis identified the variables that related significantly (r > 0.5) to the first two DCA axes gradients. Species-environment relationships were explored by direct gradient analysis using stepwise canonical correspondence analysis (CCA), to determine which available GIS-derived environmental measures best explained the gradients in species composition. Explanatory variables were added in the order of greatest additional contribution to the variance explained, but only if they were significant ($P \leq 0.01$). Significance was determined using Monte Carlo permutations. A minimal subset of uncorrelated environmental variables was chosen, which explained species composition for each community, with a maximum of three variables selected.

A comparison between CCA and DCA eigenvalue scores showed how well environmental variables were able to account for variation in the floristic data and

to suggest if important environmental variables were overlooked. Intra-set correlations and the change in eigenvalues for the first and second axes were examined. Maps representing the spatial distribution of the first two DCA axes scores were generated for each community.

III. RESULTS

Table 2 presents the eigenvalues for the first two axes of the DCA relative to the CCA axes that were constrained by the selected set of environmental variables. Eigenvalues were moderately higher for DCA than for CCA in all communities, indicating that a portion of the species variation was not accounted for by the explanatory variables in CCA. However, there

are strong correlations for most of the communities between DCA axis 1 and the explanatory variables (Table 3), suggesting that much of the variation in species composition is related to the selected environmental variables.

Chaparral

Table 2. Eigenvalues for DCA axes and CCA axes.

Community	DCA_1	CCA_1	DCA_2	CCA_2
Chaparral	0.46	0.41	0.19	0.18
Coastal Sage Scrub	0.50	0.48	0.11	0.09
Foothill Woodland	0.30	0.27	0.19	0.16
Yellow Pine Forest	0.31	0.26	0.29	0.22

Table 3. Variables having highest Pearson correlation (Pr) with DCA axes.

Community	DCA Axis	Summary Statistic	Environmental Variable	Pr
Chaparral	1	Maximum	Maximum summer temperature	0.93
	1	Maximum	Mean annual temperature	0.82
	2	Maximum	Seasonality of temperature	0.69
	2	Mean	Seasonality of precipitation	0.63
Coastal Sage Scrub	1	Mean	Mean annual precipitation	0.95
	1	Mean	Seasonality of precipitation	0.92
	1	Maximum	Mean annual temperature	0.89
	2	Mean	Min. winter temperature	0.77
Foothill Woodland	1	Maximum	Max. summer temperature	0.92
	1	Maximum	Mean annual temperature	0.73
	2	Mean	Seasonality of precipitation	0.86
	2	Mean	Mean annual Precipitation	0.75
Yellow Pine Forest	1	Mean	Seasonality of temperature	0.62
	1	Maximum	Max. summer temperature	0.60
	2	Maximum	Seasonality of precipitation	0.70
	2	Minimum	Elevation	0.69
	2	Minimum	Mean annual precipitation	0.62

Table 4. Pearson correlation (Cr) of selected environmental variables with CCA axes.

Community	CCA Axis	Summary Statistic	Environmental Variable	Cr
Chaparral	1	Maximum	Maxiumum Summer temperature	-0.95
	2	Maximum	Seasonality of temperature	-0.93
Coastal Sage Scrub	1	Maximum	Annual precipitation	0.96
	2	Mean	Winter minimum temperature	-0.93
Foothill Woodland	1	Maximum	Maximum summer temperature	0.95
	2	Mean	Seasonality of precipitation	-0.91
Yellow Pine Forest	1	Mean	Seasonality of temperature	0.63
	2	Maximum	Elevation	0.78
	2	Minimum	Seasonality of precipitation	0.62

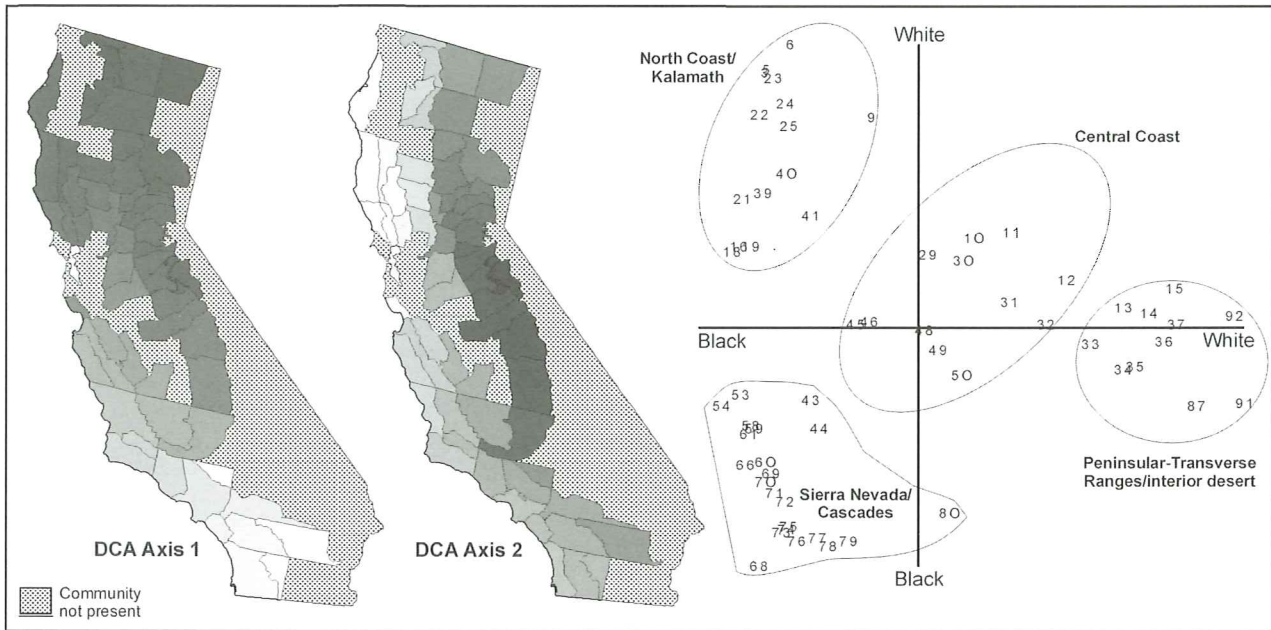Note: $P < 0.01$ for all chosen variables from Monte Carlo simulations.

Figure 2. DCA results for chaparral, where biplot numbers represent the respective subregions
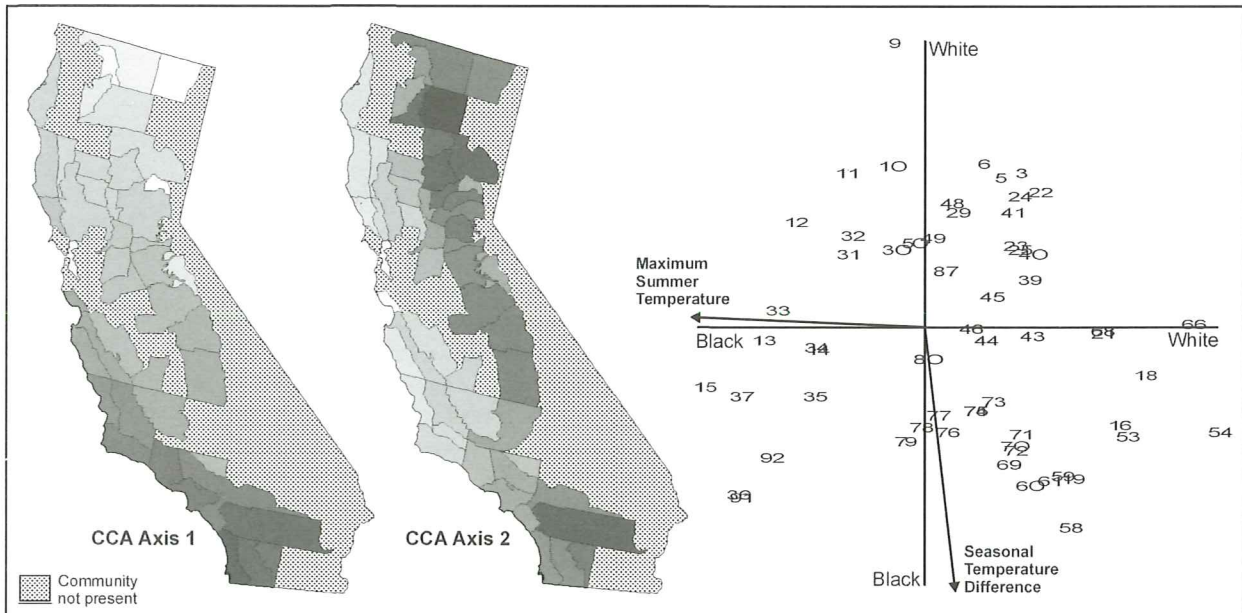

Figure 3. CCA results for chaparral, where biplot numbers represent the respective subregions.

DCA explained 65% of the cumulative variance in plant species found in the chaparral community, while the first two CCA axes explained 59% of the variance when constrained by the selected environmental variables (Table 4). There are four major chaparral groups represented by the results: Kalamath/North Coast Ranges, Sierra Nevada/Cascades, Central Coast, and South Coast Ranges/Peninsular-Transverse Ranges/ interior desert (Figure 2). The first DCA axis captured considerable floristic turnover along latitude. The dominant gradient represents a shift from the more xeric species associated with chaparral in the

Peninsular-Transverse Ranges, South Coast Ranges, and interior desert to the more mesic areas of the Sierra Nevada/Cascades Ranges and Kalamath/North Coast Ranges. Rainfall has been noted to have a strong influence on chaparral (Hanes [15]), but was not found to be an important factor in describing the diversity among subregions. The main variable identified for the first CCA axis was maximum summer temperature. It appears at this scale of observation, that floristic turnover relates best to a gradient of relative heat stress that may in turn affect the available water balance (Table 4). Ignoring the inversion of output weights, the maps for the first axis in Figures 2 and 3

show only minor differences in the patterns of subregion scores between DCA and CCA. The only other environmental variable that correlated well with the first DCA axis was mean annual temperature (Table 3).

The second DCA axis describes a variation from the northwest region, southeast to the southern Sierra Nevada Range. The seasonal temperature difference was identified for the second CCA axis (Table 4) and was most closely correlated with the second DCA axis as well (Table 3). The magnitude of temperature change between seasons captures much of the pattern in species composition from the mild coastal climates of the northwest to highly variable montane

climates. Again, the maps of the second axis in Figures 2 and 3 correspond fairly well. The constrained CCA axis shows the greatest discrepancy in the subregions located north and south of San Francisco Bay. Patterns in the Sierra Nevada range are also less homogenous in the CCA results. In addition to the variable selected for CCA axis 2, the seasonality of precipitation showed a moderate correlation with the second DCA axis.

Coastal Sage Scrub

DCA axes explained 61% of the cumulative variance in plant species found within the coastal sage scrub community, and CCA axes explained 57% of the cu-
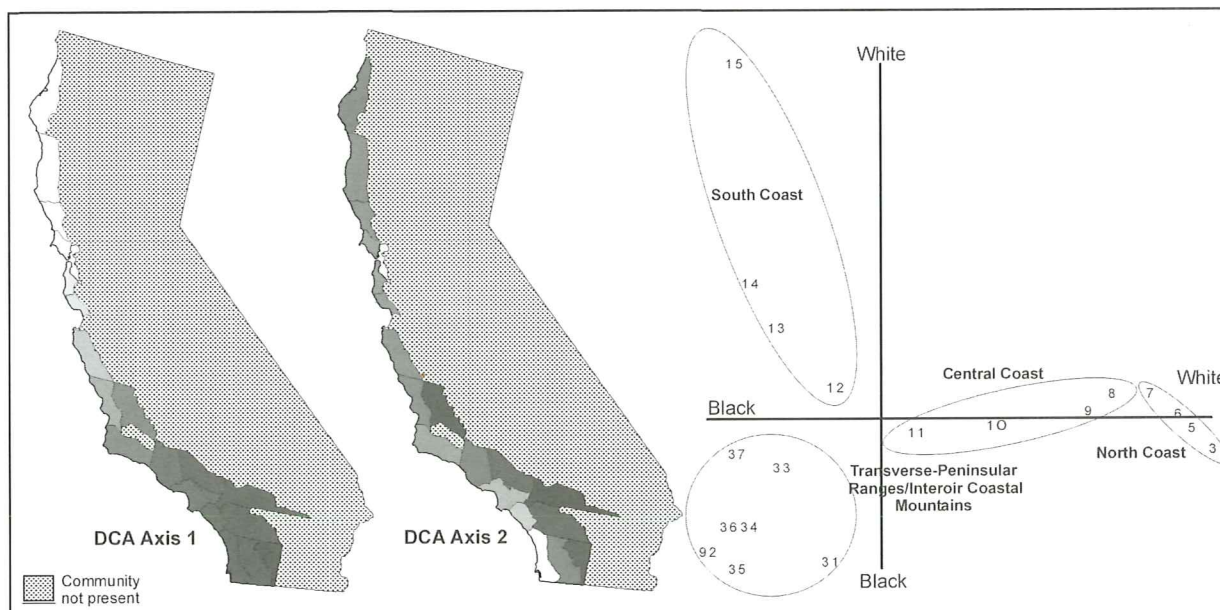

Figure 4. DCA results for coastal sage scrub, where biplot numbers represent the respective subregions.
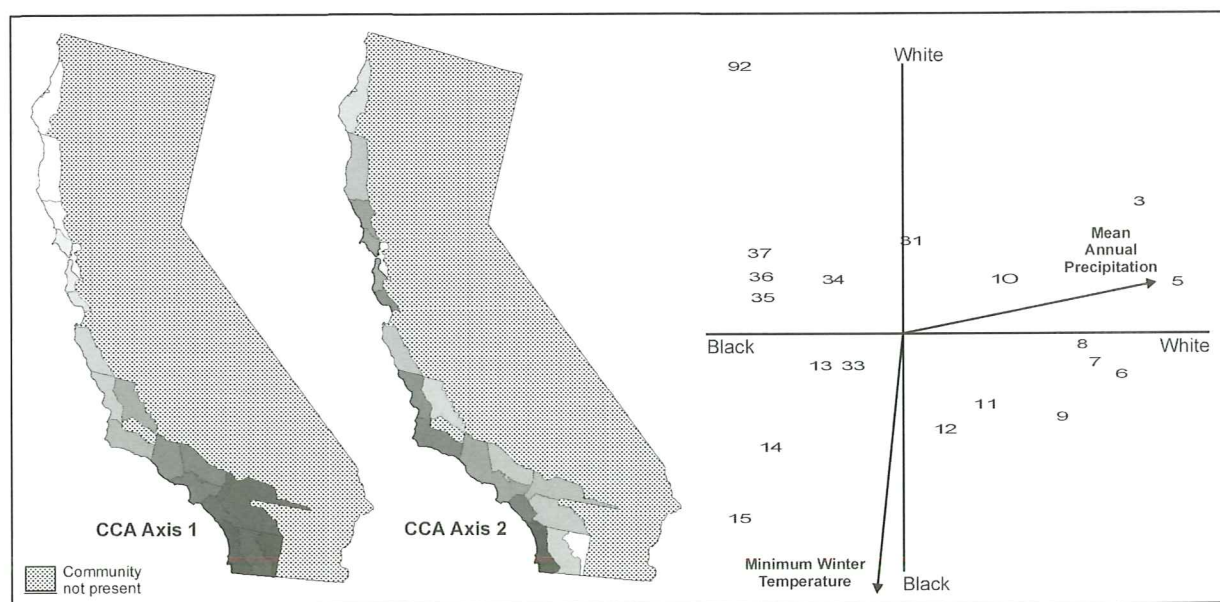

Figure 5. CCA results for coastal sage scrub, where biplot numbers represent the respective subregions.

mulative variance in species-environment relationships. The first axis describes considerable floristic variation between border regions of the Central Coast Ranges and the Transverse-Peninsular Ranges (Figure 4), as described by Mooney [28] and Heady et al. [18]. The first axis illustrates three phases: northern coastal scrub, central coastal scrub, and southern coastal scrub. This axis reflects a decrease in evergreen species with increasing aridity and a progressive increase in drought-deciduous and succulent species (Mooney [28]). The mean annual precipitation was chosen as the single best variable for CCA axis 1 (Table 4). The relative pattern of subregion scores for the first axis is seen to be similar in the maps of Figures 4 and 5, except for an inversion in the two northernmost subregions. This deviation is unexpected and

may be due to a problem with the interpolated climate data, since annual precipitation would be expected to follow a smooth latitudinal pattern along the coast as well. The coastal sage scrub that is found within these two subregions have landscape differences: the coastal sage scrub in subregion 3 is on a broad coastal plain, and subregion 5 is on the steep slopes of the Mendicino Coast Ranges. Therefore, the discrepancy could be explained by an orographic increase in precipitation overriding a latitudinal gradient. In addition to the variable selected by CCA, the seasonality of precipitation showed a very strong correlation with the first DCA axis (Table 3).

The subregion scores for the second DCA axis (Figure 4) are driven in large part by local endemics and Baja
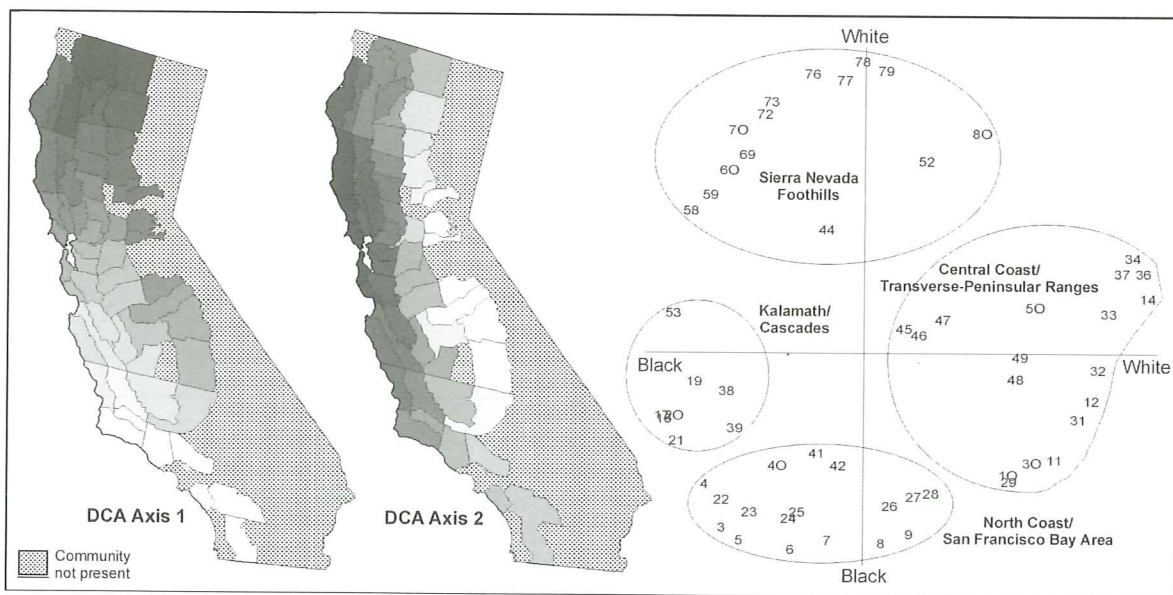

Figure 6. DCA results for foothill woodland, where biplot numbers represent the respective subregions.
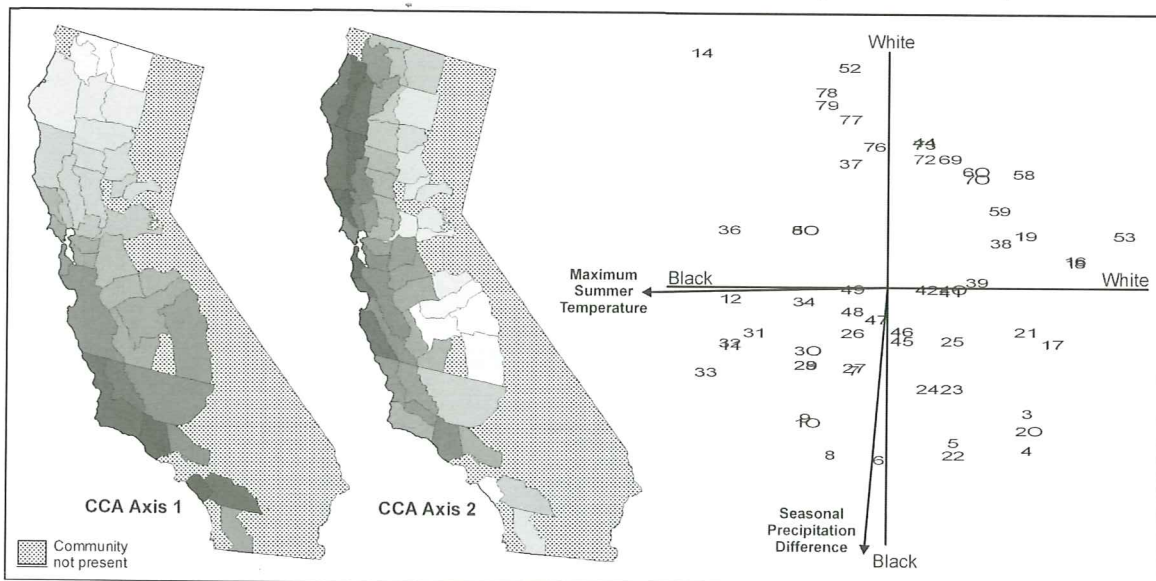

Figure 7. CCA results for foothill woodland, where biplot numbers represent the respective subregions.

California components in the flora of the south coast, primarily San Diego County (Westman [51], Westman [52]). The gradient of the second axis contrasts this most strongly with interior stands of coastal sage scrub that differ in composition from the coastal stands (Harrison et al. [17]). Though the subregion scores are inverted, a very similar pattern is seen for the second CCA axis (Figure 5), as would be expected given the strong correlations seen with selected DCA variables in Table 3. The variable selected for the second CCA axis was mean annual temperature, most likely reflecting a turnover in species related to heat stress as one moves away from the coast (Westman [51]). The minimum winter temperature also shows a moderate correlation with this axis, reflecting the increased fluctuations in temperature of interior regions as well.

Foothill Woodland

DCA axes explained 49% of the cumulative variance of the plant species found in the foothill woodland community, and CCA axes explained 43% of the cumulative variance of species-environment relationships. The first DCA axis reflects a gradient in moisture stress from the xeric *Quercus* spp. woodlands in southern California and the Central Coast to the more mesic stands of the northern central west coast, and Kalamath/Cascades (Figure 6). The maximum summer temperature was selected for the first CCA axis (Table 4) and is very closely related with the first DCA axis (Table 3). This similarity is seen in comparing relative differences in maps of first axis subregion scores in Figures 6 and 7, after compensating for the inversion of the weighting scheme. In addition to maximum summer temperature, the mean annual temperature showed a fairly strong relationship to the first DCA axis.

The second DCA axis reflects the change in species composition from coastal stands to the interior Great Central Valley foothills and southwest interior valley stands (Figure 6). The *Quercus* spp. woodlands have little floristic unity except for the ubiquitous annuals in their ground cover. Species from adjacent grassland, chaparral, and coniferous forest communities associate with the foothill woodland community over a wide range of physiographic and climatic situations, contributing to compositional changes. The seasonality of precipitation, trending east to west, was selected for the second CCA axis (Table 4). The correspondence between CCA and DCA results is fairly good for axis 2, except for strong differences in subregions 14 and 37 on the southern coast (Figure 6 and 7). This may be related to some degree of similarity between the effects of latitude and continentality on the seasonality of precipitation. However, it is also possible that this may be related to some problem with the inter-

polated climatic data. In addition to the seasonality of precipition, annual precipitation was also strongly correlated with the second DCA axis (Table 3).

Yellow Pine Forest

This community is probably Munz and Keck's [29] broadest category and to treat it as a single entity presents many problems. DCA axes explained 60% of the cumulative variance in the plant species found in the yellow pine forest community, while two CCA axes explained 48% of the cumulative variance. The first DCA axis represents a broad south-north transition of the Transverse-Peninsular/Central Coast Ranges, Sierra Nevada/Casacades, North Coast Range/ Kalamath, and the Modoc Plateau/eastside Sierra Nevada (Figure 8). This pattern denotes several environmental gradients within this broadly classed community. This includes a variety of north-south gradients associated with elevation, xeric versus mesic conditions, and seasonality in temperature and precipitation. The seasonal temperature difference was selected for the first CCA axis (Table 4) and is most strongly associated with the first DCA axis (Table 3), though the correlation with the first DCA axis was the lowest of the four communities studied at 0.62. As a result, there are some greater discrepancies in the maps of first axis scores seen in Figures 8 and 9, with differences extending primarily from the Central Coast to the mountains of the southern interior. The only other variable that had a moderate passive correlation with the first DCA axis was the maximum summer temperature.

The second DCA axis appears to be driven by changes in species composition from the northern coastal zone to the area east of the Sierra Nevada mountains (Figure 8). This corresponds to a strong gradient in the amount and variability of temperature and precipitation and may reflect the appearance of species associated with the Great Basin region (Rundel et al. [42], Thorne [46]). Elevation and the seasonality of precipitation were both selected for the second CCA axis (Table 4), each having approximately the same correlation with the second DCA axis (Table 3). Even when using two variables to constrain the second CCA axis, the pattern of subregion scores seen in Figures 9 and 10 diverge substantially.

The grouping of the "yellow pine" indicator species, i.e. *Pinus ponderosa, Pinus coulteri,* and *Pinus jeffreyi,* by Munz and Keck [29] poses many problems (Haller [14]), but has provided some insight into the complexities of the lower montane mixed coniferous forest communities floristic diversity. The DCA examination did elucidate four floristic groups, with their own internal floristic variation: Kalamath/North Coast Ranges,
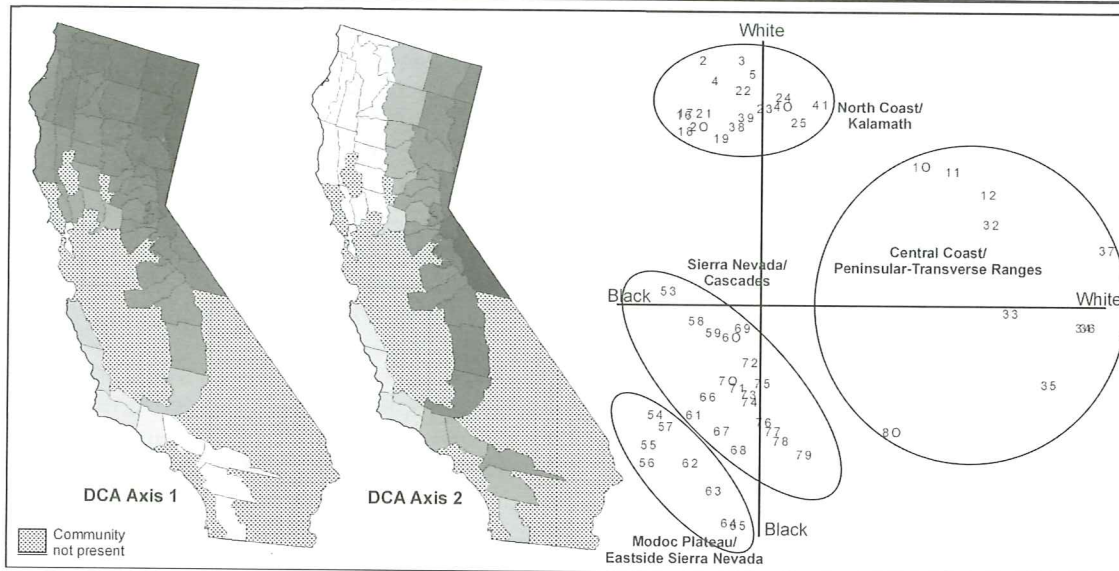
Figure 8. DCA results for yellow pine forest, where biplot numbers represent the respective subregions.
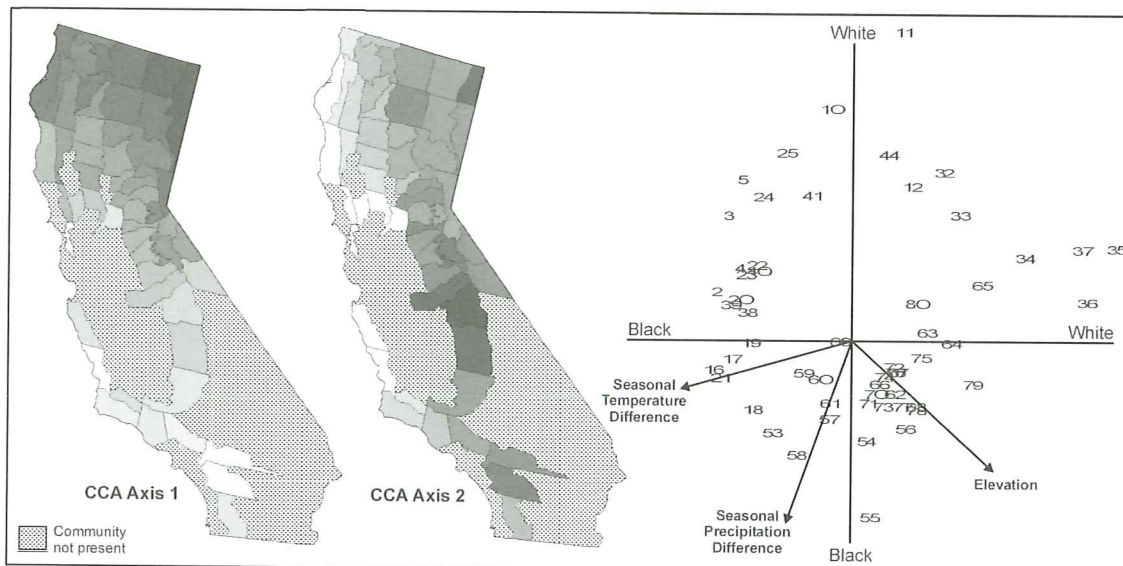

Figure 9. CCA results for yellow pine forest, where biplot numbers represent the respective subregions.

Cascade/Sierra Nevada Ranges, Modoc Plateau/ eastside Sierra Nevada, and the Central Coast/Trans- verse-Peninsular Ranges. However, the physiogno- mic similarities among the indicator species does not warrant them being grouped as a single vegetation type they should be treated separately because of the complex environmental gradients and significant eco- logical differences. The compositional gradients elu- cidated by DCA are much too complicated to explain using the available environmental measures in a CCA analysis.

IV. DISCUSSION

Though derived from coarse-scale regional datasets,

the CCA results are consistent with past studies on the species-environment relationships developed from fine-scale field plot data over regional extents for chap- arral (Hanes [15], Keeley and Keeley [21], Schoenherr [43]), coastal sage scrub (Westman [50,51], Westman [52], Mooney [28]), foothill woodland (Griffin [13], Schoenherr [43]), and yellow pine forest (Haller [14], Rundel et al. [42], Thorne [46], Parker [34]).

Seasonal variability and climatic extremes were gen- erally more effective in explaining coarse-scale spe- cies gradients for each community than mean annual climatic conditions, except for coastal sage scrub and the inclusion of elevation for yellow pine forest. Nev- ertheless, dominant species gradients were generally associated with a maritime versus continental pat-

tern and growing season moisture stress, climatic gradients that integrate elements of both temperature and moisture. These findings are comparable to Ohmann and Spies [32] study of Oregon coniferous forests. The species gradients for all communities across California were much more strongly associated with moisture stress during the hot, dry summers than with winter conditions, along a characteristic latitudinal gradient. This association was consistent with observations in Oregon (Ohmann and Spies [32]), the southern Rockies (Allen et al. [2]), and the northern California Sierra Nevada/Cascade axis (Parker [34]). The results supported our hypothesis of the primary importance of macroclimate controlling regional compositional gradients in these four plant communities.

An exhaustive record of regional floristic composition is practically impossible to obtain using even numerous field plot data. The large sampling error in small plots relative to total species present in a given landscape can only be compensated for by collecting a very large number of plots or sampling an area over considerable time to acquire species variation information in relation to differing environmental situations (Preston [37]). This approach was successfully demonstrated by Ohmann and Spies [32], however their 2,443 fine-scale field plots only accounted for a maximum of 181 species. The long time frame and spatial sampling contained in a biological atlas can provide a near complete inventory for a region. A comprehensive floristic atlas can provide the generalized spatial information needed for conducting regional ecological analysis for proposed coarse-scale land characterization projects (Brown et al. [3]). Using ordination analysis to analyze the coarse-scale spatial information found within a floristic atlas with coarse-scale environmental data in a GIS we can obtain insights into the mechanisms responsible for regional patterns of vascular plant diversity. These insights may not be fully realized in fine-scale studies, even if conducted at a regional extent.

The number of sites where a species will be found with a fixed sampling scheme is a monotonically increasing function of the average abundance of the species (Hanski et al. [16]). Despite a large number of field plots, studies such as that conducted in Oregon (Ohmann and Spies [32]) are still surprisingly species poor, representing 181 species compared to our 558 to 1478 species. Ohmann and Spies [32] postulated that the rare species would increase total variation in the species-by-plot data matrix, but that their presence is unlikely to be explained by environmental variables. This reasoning was used to explain their low values for total explained variation. Our findings do not agree, as our explained variation was 43-59% across entire communities that generally cover the

entire state (Figure 1), and CCA eigenvalues were generally close to those produced by the unconstrained DCA. While locally rare species or succesional species are more difficult to detect spatially and temporally, a floral atlas will allow them to be associated with more generally defined plant communities. Our findings show that species presence-absence strongly influences regional-scale ordinations, where gradients are long and the use of a floral atlas includes a number of succesional (short presence on landscape) and rare species.

By using a comprehensive floral atlas, our effort has been able to capture and explain complex species diversity gradients, but not without problems. While there is a greater capacity to handle rare or succesional species with a coarse-scale floristic atlas, this approach will typically result in a relatively low number of samples from which to derive the environmental gradients. The discrepency in more specific quantitative results (e.g. variance explained, eigenvalues) between our study and others (e.g., Ohmann and Spies [32], Westman [51]) may be due to different sample sizes used, even though similar environmental conclusions were reached. For example, Ohmann and Spies [32] used fine-scale field plots, while our study used irregularly sized subcounty regions with an average size of 4,354 km². This may bring into question the robustness of our environmental relationships. Recognizing the sensitivity of the results of spatial analyses to the definition of units for which data are collected is critical to characterizing landscapes with minimal bias and avoidance of spurious relationships (Jelinski and Wu [20]). The effect of data aggregation on geographic analysis, known as the modifiable areal unit problem (Openshaw and Taylor [33]), can lead to different data inferences depending on the scale of aggregation. In this study the size of the subregion for which plant species data is recorded is much larger than the mapped community found within its boundary, and the environmental statistics were calculated by aggregating community patches. The aggregation of spatial data involves a smoothing effect, averaging over variations, but it allows one to make more definitive states about a complex system.

V. CONCLUSIONS

From the discussion in the previous sections, the problem of scale in community analysis is not really a "problem", *per se*, if recognized and dealt with explicitly. Our ability to sample environmental heterogeneity depends on the scale and time frame of our measurements. Coarse-scale databases constitute not only a valuable resource for decision making, but also a tool for researchers attempting to understand geo-

graphic patterns of diversity. Frequently, these databases are assembled from a compilation of museum records, local collecting trips and identification books, and as such were probably never made for robust analyses (Fagan and Kareiva [9], Pendergast et al. [36]). Yet, these databases and their sampling methdologies (e.g. subregions, counties, etc.) are the common biodiversity databases available for decision making and research (Scott et al. [44]). Whether they are corrected for their sampling problems (Fagan and Kareiva [9]), or not (Lawton et al. [23]), they still provide a wealth of previously unused biodiversity information for ecological modeling.

The methods employed in this research effort have been developed to quantify regional changes in floristic composition arising from the environmental gradients found in the state of California. As such, the methods and the use of generalized data from a floristic atlas rather than fine-scale field plot databases may not be expected to provide the most relevant information for floristic provinces which operate under different processes (multi-scaled controls) or for the needs of localized decision making. However, initial results of these methods are encouraging and show promise as a component of a regional and global characterization of plant biological diversity, especially in relation to the potential impacts of climatic change (Fairbanks et al. [10]).

Coarse-scale analyses are simplifications of naturally heterogeneous systems, but they can present us with useful information from which to derive questions and to further refine our understanding. Our results agree with previous fine-scale studies (e.g., coastal sage scrub, chaparral, and foothill woodland) and raise further questions on the complexity of macroecological patterns of biodiversity (e.g. yellow pine forest). However, the results of this study are affected by the ambiguity of the Munz and Keck [29] vegetation categories, generalized species ranges, and errors in the GIS-based environmental data sets.

This work does allude to the potential error in treating communities as homogeneous units in climate change scenarios and regional conservation planning. For example, the strategy of treating yellow pine forest as a homogenous unit in the landscape with a single environmental response function is shown to be quite flawed. While this has been obvious to the terrestrial ecology community for some time, the global-scale modeling community should be made aware of where the assumption of homogeneity is either more or less of a problem. Root and Schneider [41] have proposed that ecologists and climatologists work together at a coarser scale to avoid the mismatches in scale that have made much of the global change work

obsolete. Working within plots the size of tennis courts will not help those trying to construct coarse-scale models of climate change or coarse-scale land characterization efforts, however the effect of data scale on interpretation must be addressed. The analysis presented here provides a quantitative mechanism to infer how characteristics of a vegetation type may change in response to environmental forcing functions (Fairbanks et al. [10]).

This analysis represents an examination of using coarse-scale species distribution and community distribution data within direct gradient analysis models. Regional patterns of variation in species composition were complex and multidimensional, denoting the well-known uniqueness of the California floristic province. Many environmental factors contribute to the floristic composition of a region, and it cannot be expected that all relevant information can be anticipated or even fully represented in a GIS database. However, by examining those regions that are not explained well by the current efforts, future research can be targeted to better understand unique or localized effects on floristic diversity.

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