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LOCAL SCALE VEGETATION MAPPING AND ECOTONE ANALYSIS IN THE SOUTHERN COAST RANGE, CALIFORNIA

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ABSTRACT

Plant communities in the southern Coast Range of California form a mosaic with discrete to gradual transitions between multiple vegetation types. To accurately portray this pattern and to quantify the areal coverage of ecotonal space, a new method of mapping vegetation was developed. Vegetation stands were classified and mapped in separate GIS layers to the full extent of their respective suite of indicator species. Since all stands were mapped in this way, the overlap of different communities in the GIS represents ecotonal space. Vegetation mapping was entirely ground-based using a GPS receiver. Vegetation classification followed the Holland and Keil scheme. Eleven plant communities were identified within the 92.6 ha study area. This mapping method revealed that 32% of the total area was ecotonal and that the majority of plant communities exhibited a greater portion of their total area as ecotone than as discrete space. This finding suggests that typical vegetation maps depicting discrete boundaries between all vegetation types may misrepresent a nontrivial proportion of the area mapped. In addition, because ecotones are ecologically significant and important to conservation, the portrayal of transitional space between communities is worth consideration in the future creation of vegetation maps within California.

Key Words: ecotone, full extent, fuzzy boundary, multi-layer mapping, semi-stand, serpentine, vegetation classification, vegetation map.

The study of ecological boundaries has played an important role in developing the field of ecology. Research in this topic is diverse and has ranged from exploring small-scale boundaries at the root soil interface (Belnap et al. 2003) to large-scale boundaries across continents (Thompson et al. 2005; Peinado et al 2007). One of the most common terms used to express ecological boundaries is the ecotone. The liberal usage of ecotone in the literature has spurred many attempts at reclassification and introduction of new vocabulary (Kent et al. 1997; Holland 1988; Strayer et al. 2003). For the purposes of this study, ecotone is the transition between adjacent plant communities, as first defined by Clements (1905).

Because ecotones are the product of adjacent plant communities, the plant community concept is central to the concept of the ecotone (Kent et al. 1997). While Gleason (1926) used ecotones as part of his argument against the existence of plant communities and while ongoing debate over plant community concepts still exist (reviewed in Tansley 1920; Austin 1985; Mucina 1997), most vegetation scientists at least acknowledge the usefulness of recognizing plant communities and the narrow to broad transitional zones between them (Barbour et al. 1999). Ecotones may be the result of various phenomena (Lloyd et al. 2000) such as anthropogenic and natural disturbances (Cadenasso et al. 2003), abiotic and biotic environmental gradients (Walker et al. 2003), and biological invasion fronts (Hoffman et al. 2004).

Much has been learned about basic ecology through the investigation of ecotones (Austin 1985; Gosz 1993; Smith et al. 1997; Kark and van Rensburg 2006). Nevertheless, these transitional spaces have often been overlooked by vegetation scientists who tend to focus on discrete, repeatable vegetation types (Risser 1995; Mucina 1997). This focus on discrete vegetation is also reflected in the field of vegetation mapping (Küchler 1988a; Goodchild 1994). Nearly all paper or digital vegetation maps depict two-dimensional orthographic canopy cover with complete coverage by non-overlapping polygons. An obvious drawback of this typical approach is that vegetation stand boundaries are depicted more discretely than they actually are in the field. As a result, information about the extent and composition of ecotones is lost and this renders the vegetation map less accurate.

The goal of this study was to describe and analyze the plant communities and ecotones of a nature reserve in Poly Canyon, located in the southern Coast Range of California (Fig. 1), through the use of a high-resolution, multi-layer approach to local ground-based vegetation mapping. This detailed approach resulted in several noteworthy mapping unit categories: those being *full extent*, *discrete*, *ecotone*, *semi-stand*, and *total*

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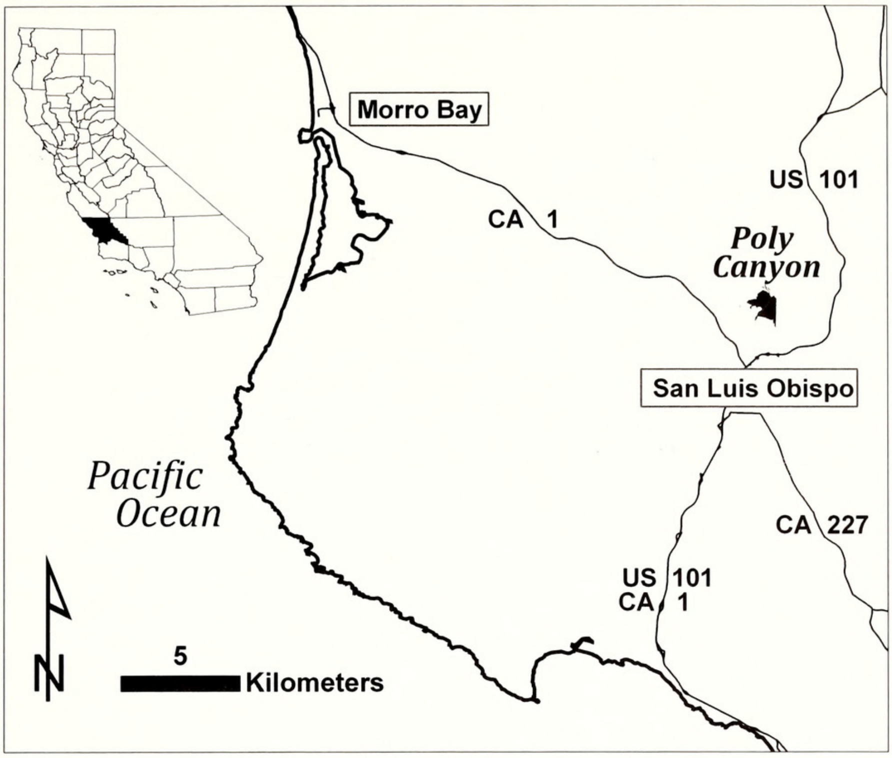

FIG. 1. Location of study area in San Luis Obispo County, CA.

overlap (Fig. 2). Full extent corresponds to a complete stand, including the discrete portion, and if present, the ecotone portion. The discrete portion of a stand represents the distinct and definable area that clearly embodies a classified plant community or vegetation type. Ecotone represents the area of overlap between two or more plant communities, as mentioned previously (Fig. 3). Semi-stands represent a partial/incomplete "stand" of one plant community, lacking any discrete space of its own, that is entirely within the matrix of a different plant community (Figs. 2 and 3). A semi-stand together with the matrix community resembles an ecotone in structure and species composition. The term matrix is used here to represent the background vegetation with its own unique structure or composition (Forman and Godron 1981) from the semi-stand that is within it. Total overlap represents all areas that are not one discrete vegetation type and is calculated by the sum of ecotone and semi-stand areas. Specifically, we wanted to determine the amount of full extent, discrete, ecotone, semi-stand, and total overlap area that each vegetation type occupied, discover which vegetation types shared the greatest amount of ecotone and total overlap area with other vegetation types, and measure the ecotonal and total overlapping space of the study area.

STUDY SITE

The 93 ha study area is centered near 35°19′N, 120°39′W (WGS84) within Poly Canyon, a 510 ha natural area NNE of and adjacent to the core campus of California Polytechnic State University, San Luis Obispo, in San Luis Obispo County (Fig. 1). Poly Canyon lies along the southwest foothills of the southern Santa Lucia Range, part of the larger southern Coast Range. The canyon is formed from two northeast-to-southwest trending ridgelines flanking Brizzolara Creek, a seasonal tributary of Stenner and San Luis Obispo Creeks. Many hillside springs and seeps feed the seasonal flow. Elevations range from around 120 to 345 m. The general slope of both canyon sides is about 20° (36%) with steeper local inclines to 45° (100%). Soils within the study area are mostly of the Los Osos Loam series, Lodo–Diablo Clay Loam complex, Los Osos–Diablo complex, Rock Outcrop–Lithic Haploxerolls complexes (serpentine), and Obispo–Rock outcrop complexes (serpentine) *sensu* Ernstrom (1984).

Climate is a cool summer phase of the dry-summer subtropical ("mediterranean") type of humid mesothermal climates (Trewartha 1968; Yahr 1961). Winter high temperatures average near 18°C, lows average around 6°C. Summer high temperatures average near 25°C, with average lows near 11°C. The lowest temperature recorded on the adjacent core campus was −12.7°C and the highest was 44.4°C. Precipitation falls as rain primarily from October through April, and averages about 558 mm per year. Typically, less than 25 mm of precipitation is recorded from 1 May to 30 September, but overnight and morning fog with near 100% humidity occurs nearly every night unless drier,

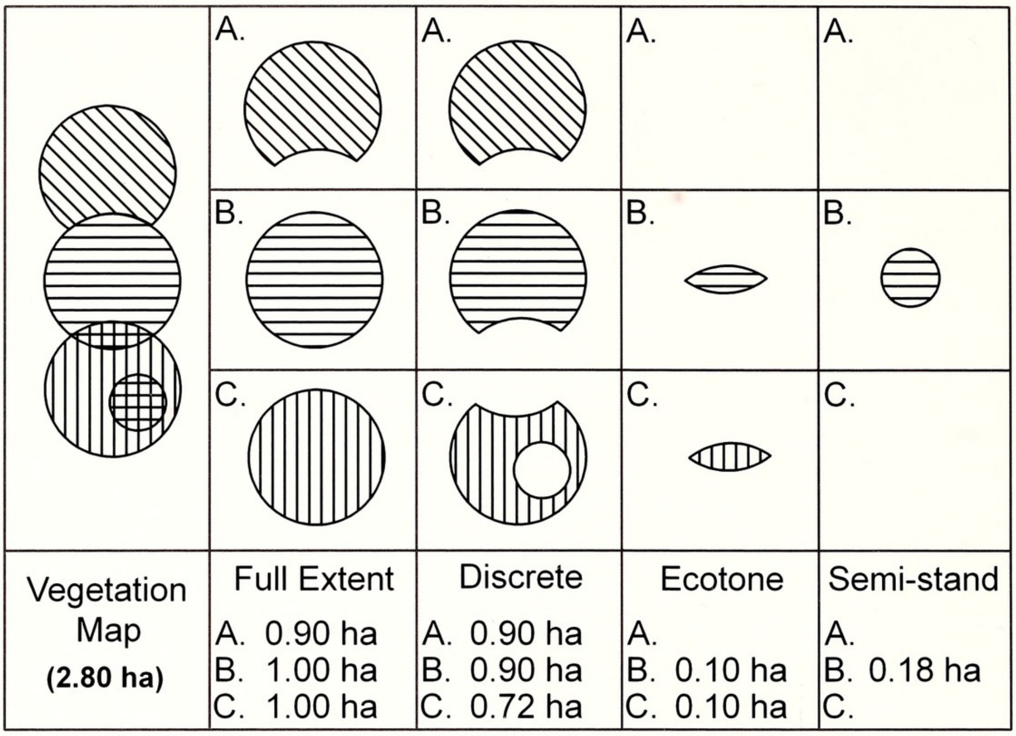

FIG. 2. Hypothetical vegetation map, composed of three plant communities (A, B, and C), depicting defined map units utilized to describe the vegetation of the study area.

down-sloping winds descend from the Salinas Valley over the Santa Lucia Range to overwhelm the onshore flow of marine air (Felton 1965; WRCC 2006)

Poly Canyon exhibits high vascular plant diversity with over 400 species collected thus far (De Rome 1997). Within the study area rare plants are present, such as the local serpentine endemic *Calochortus obispoensis* (De Rome 1997). Typical serpentine indicators (Safford et al. 2005), such as *Quercus durata* var. *durata*, are also frequent. The vegetation of the study area is composed of numerous plant communities, which are described later in this study.

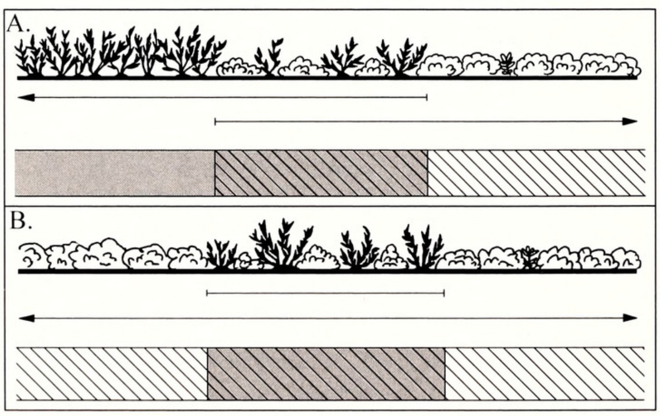

FIG. 3. Hypothetical ecotone and semi-stand scenarios and corresponding representative GIS polygon overlap. A. Ecotone between Mixed Chaparral (left-side w/corresponding gray GIS polygon) and Southern Coastal Scrub (right-side w/corresponding striped GIS polygon). B. A semi-stand of Mixed Chaparral occurring in a Southern Coastal Scrub matrix.

METHODS

The relatively low cost and high precision of using GPS (Geographic Positioning System) and GIS (Geographic Information System) technologies (see Foster 1993) is now ideal for a high resolution, multi-layer approach to vegetation mapping where stands (patches of a particular plant community) are defined by a suite of indicator species that are mapped to their fullest extent in separate layers. Since plant communities integrate, forming gradual to abrupt ecotones across the landscape, they can be individually separated into layers of a GIS. This approach avoids the arbitrary or inconsistent definitions of stand boundaries that can result from creating one integrated map that portrays stands as entirely discrete and not overlapping. Portraying plant communities and ecotones in this way is precise and feasible at the local scale (e.g., hillside, small nature reserve, rancho, etc.).

Distinct plant communities were classified and mapped in this study following the Holland and Keil (1995) plant community classification scheme and this multi-layer, full extent mapping approach. Dominant species from the following categories: tree, shrub, forb, and grass, were also recorded for each individual stand mapped and used to further describe the communities and to provide a cross-reference to vegetation series in the Manual of California Vegetation (Sawyer and

Keeler-Wolf 1995). Ecotones among the eleven distinct communities were mapped as the overlap of their respective polygons in the different GIS layers (Figs. 2 and 3). The areas of overlap were then used to quantify community and ecotone characteristics within the study area using a GIS. Methodology of the vegetation classification, mapping, and ecotone analyses are described in the following sections.

Vegetation Classification

The Holland and Keil (1995) plant community classification scheme was used to classify the vegetation of the study area. This classification scheme distinguishes plant communities primarily on physiognomy and secondarily on species composition. Habitat characteristics are also incorporated when they will increase usefulness (e.g., coastal sand dune communities, marine aquatic communities, riparian, vernal pool). This classification scheme is not all-inclusive of the plant communities found in California but does provide a logical framework that is helpful for classifying vegetation.

During spring 2001, the study area was traversed by foot to produce a list of plant communities present. Stands encountered were examined for physiognomy and dominant species composition by carefully walking throughout the discrete portions of each stand. Dominant species were defined as those plant species that contributed the greatest cover (Barbour et al. 1999) based on ranked percentage cover estimates (Daubenmire 1959; Mueller-Dombois and Ellenberg 1974). Once dominant and subordinate species were recorded for a stand they were compared to community descriptions in Holland and Keil (1995) and classified accordingly. The list of plant communities was then formatted as a data dictionary and uploaded into the GPS datalogger for use in mapping and classifying vegetation polygons in the field.

Vegetation Mapping

Area Subdivision. Mapping began spring 2001 and was completed by spring 2002. The study area was split into eight subareas that roughly followed the four major slopes (N-, E-, S-, and W-facing slopes) of the two prominent hills/ridgelines of the study area. Mapping priority fell to stands located on the perimeter of the study area within each subarea since these stands typically had less integrating neighboring stands, and because it was easier to keep track of species composition and reference vegetation patches upslope than downslope. Interior (uphill) stands within a subarea were subsequently mapped until the subarea was completed. All stands within a subarea were mapped before moving on to an adjacent subarea.

Mapping Units. No exact minimum mapping unit was defined before mapping began but general guidelines were established based on two factors: the physiognomy of the stand, and the context it occurred in. In regard to physiognomy, minimum vegetation units generally increased in size by herb-, shrub-, and tree-dominated stands, respectively. For example, the minimum mapping unit of Valley and Southern Coastal Grassland was smaller than that for Coast Live Oak Woodland because some stands of Valley and Southern Coastal Grassland could be the size of the canopy of one large coast live oak tree. On the other hand, a single large coast live oak tree in the middle of Valley and Southern Coastal Grassland could not be considered Coast Live Oak Woodland even if it occupied the same or a bigger areal extent as a patch of grassland because it was only one individual and not an assemblage. In regard to context, if a patch of vegetation appeared to form a distinct stand based on physiognomy and species composition compared to adjacent patches, then it was mapped.

Indicator Species. Stand-specific indicator species were determined before mapping in order to delineate the boundary of the stand (i.e., its full-extent). Indicator species were species with high cover in the stand, were distributed throughout the stand, and usually had a life form that corresponded to the physiognomy of the stand itself (e.g., shrub species in a shrubland). In a few instances, species of dissimilar life form than the stand physiognomy were also used (e.g., *Rhamnus californica*, a shrub, used as an indicator for Coast Live Oak Woodland). If an indicator species was also common within an adjacent stand it was removed from the list of indicator species.

Thus, suites of indicator species (differential species) collectively exhibit high fidelity (strong or exclusive correlation), within-stand constancy (continuous presence), and area-of-occupancy within discrete vegetation associations (*sensu* Braun-Blanquet 1965; Kent and Coker 1992), and are uncommon or absent in adjacent associations. Sometimes, only one indicator species met these criteria, but often several species were needed. The suite of indicator species was stand specific and not all stands classified as the same plant community were necessarily represented by the same suite of indicator species.

Semi-stands. Semi-stands are a low density patch, lacking any discrete space of their own, and composed of one or more species typical of one community that is located entirely within another community. The resulting mix of species from both the community representing the semi-stand and the community representing the matrix resembles an ecotone in structure and species composition. In these cases, the low density patch of species (semi-stand) was mapped so that where it overlapped with the matrix community, it would represent the ecotone-like assemblage that occurred there. For example, a number of hard-stemmed sclerophylous shrub species common to the Mixed Chaparral of the study area were within a stand of Southern Coastal Scrub that was dominated by soft-stemmed drought deciduous shrubs of a relatively lower stature. Collectively, these Mixed Chaparral species did not form a discrete stand of Mixed Chaparral because their cover and density was too low, but the patch of chaparral shrubs embedded in the scrub matrix resembled the ecotone between Mixed Chaparral and Southern Coastal Scrub (Fig. 3). In this example there was no discrete area belonging to the matrix community or belonging to the community representing the semi-stand, yet quantifying discrete space was a goal for this study, so these areas could not be overlooked.

Two main possibilities for mapping this situation were considered. Either one could map the area as discrete space that represented a unique community (in this case a stand of Mixed Chaparral\Southern Coastal Scrub co-dominated by *Cercocarpus betuloides* and *Artemisia californica*) with no ecotonal space between the surrounding Southern Coastal Scrub, or one could map the low density patch of Mixed Chaparral shrubs and overlay it on the matrix patch of Southern Coastal Scrub to represent the ecotone-like assemblage. The later alternative was chosen since it was conceptually similar to the method used to map ecotonal space, because it would avoid the classification of potentially numerous new communities formed from the combinations of the eleven vegetation types found in Poly Canyon, and because it seemed likely in most of these situations that the semi-stands together with the matrix vegetation represented a successional stage from one vegetation type to another and not a static or stable vegetation type (further monitoring would be required in order to confirm this). Thus, semi-stands were classified and mapped where physiognomy and species composition within a discrete matrix patch approached characteristics of a separate plant community, mimicking an ecotone but lacking the full transition to a discrete stand of the semi-stand vegetation type.

Field Mapping Sessions. Once the plant community and indicator species had been determined for a stand or semi-stand, it could then be mapped. Master lists of plant communities and species based on field data gathered during previous inventories (De Rome 1997; Curto 2000) and this project were formatted as a data dictionary uploaded into a GeoExplorer® III (Trimble Navigation Limited, Sunnyvale, CA) mapping-grade GPS receiver used to map vegetation polygons and assign their dominant species attributes in the field. Vegetation polygons were created by slowly walking the receiver around the border of each stand while GPS positions were logged at three-second intervals. Stand borders were based on the full extent of respective suites of indicator species (Figs. 2 and 3). Mapping sessions were planned around times in the day when the GPS precisional dilution of position (PDOP) was lowest ($\leq$4) resulting in the highest positional accuracy. In a few instances, topography or a dense canopy would obstruct the GPS unit from satellite view enough that the desired PDOP was not achieved.

GPS and GIS Data Processing. GPS data were differentially corrected (horizontal accuracy $\pm$1 m) using Trimble® GPS Pathfinder® Office 2.80 (Trimble Navigation Limited, Sunnyvale, CA) before import to the GIS (ArcView®, ESRI, Redlands, CA) relative to the nearest base station at Vandenberg Air Force Base. Differentially corrected stand polygons were edited in the GIS to correct any points determined to be outliers by comparison to other points in the polygon while overlaid on background orthophotographs (which had 1 m resolution). The few stands that were partially mapped at a higher PDOP than 4 were carefully scrutinized.

Relational Species Lists. After all mapping was completed in spring 2002, lists of the top three species with the highest cover in each of the following categories: tree, shrub, forb, and grass, were created for every stand and semi-stand mapped. All polygons were revisited and the species were determined based on ranked percentage cover estimates (Daubenmire 1959; Mueller-Dombois and Ellenberg 1974). The species were recorded in rank order within each growth form category and were linked to their respective polygon on the GIS using the attribute table. Nomenclature followed Hickman (1993). This was done to establish a baseline of the dominant growth forms in each stand for future reference. In addition, the lists were used to provide basic floristic descriptions of each plant community mapped and to reconcile the plant communities classified in Holland and Keil (1995) with their respective vegetation series in the Manual of California Vegetation (Sawyer and Keeler-Wolf 1995).

Ecotone Analysis

Geoprocessing functions of the GIS (ArcGIS®, ESRI, Redlands, CA) were used to ascertain the amount of total overlap (ecotone plus semi-stand) among communities. Specifically, the union, intersect, and dissolve processes were used to create layers of discrete vegetation and total overlap for each individual stand, plant community, and for Poly Canyon as a whole, based on the eleven layers of plant communities. Where stands and semi-stands of different plant communities overlapped, the intersect process would create a new layer representing that overlap (or intersection) between the two communities. This was performed for every combination of plant communities. In addition, all of the overlap layers created were combined for each community, and for the entire study area, with the union process. The dissolve process was then used to remove boundaries within contiguous areas to form single polygons representing total overlap of the entire study area. The end products represented total overlap (ecotone plus semi-stand) for the entire study area, by plant community, and by individual polygons. Discrete space was then calculated by subtracting total overlap from the original data to determine values for the entire study area and for each plant community. To determine ecotonal area, all semi-stand polygons were deleted from copies of the shape files representing all of the plant communities. Then, the same procedure as described above was implemented with the geoprocessing functions of the GIS to obtain the amount of ecotonal area. The end product represented ecotone space for the entire study area, by plant community, and by individual polygons.

Results

Vegetation Classification

Eleven plant communities were identified using the Holland and Keil (1995) classification scheme. Descriptions of each plant community are listed below. The numbers of stands with discrete area for each plant community are written in parentheses following the name of the plant community. Species information within each description was derived from the surveys of the three most dominant species within each growth form (i.e., tree, shrub, forb, and grass), which were recorded for each stand mapped. The species data used in the descriptions were based solely on stands containing discrete area (i.e., species information from semi-stands was not used). Woody perennials that exhibited a suffrutescent or vine-like growth form were included in the forb category.

Several communities, such as Yucca\Bunchgrass Scrub, Serpentine Chaparral, and California Bay\Leather Oak Mosaic, were suspected of indicating serpentine soil in the study area based on the consistent presence of serpentine indicator species (Safford et al. 2005) and the appearance of the substrate found within their stands. While no soil samples were collected to analyze for serpentine characteristics, when stands of these vegetation types were overlaid on a soil map (Ernstrom 1984), all three were found on serpentine soils. Most Native Bunchgrass Grassland stands also overlapped with serpentine soils (serpentine bunchgrass *sensu* CNDDB 2003) but a few stands were also found in non-serpentine soils.

Finally, the corresponding *Manual of California Vegetation* (MCV) (Sawyer and Keeler-Wolf 1995) vegetation series are listed at the bottom of each description for cross-reference purposes, and are designated by "MCV". Some of the series encountered were not in the manual but were still named using the format described in the MCV. Asterisks (*) indicate those vegetation types that have not been previously described by Holland and Keil (1995), Sawyer and Keeler-Wolf (1995), or by other classifications or studies (i.e., Epling and Lewis 1942; Munz and Keck 1949; Thorne 1976; Kirkpatrick and Hutchinson 1977; Paysen et al. 1980; Westman 1983; Holland 1986; Barbour and Major 1988; Desimone and Burk 1992; Rodriquez-Rojo et al. 2001; CNDDB 2003).

Valley and Southern Coastal Grassland (11) – Dominated by various nonnative annual grass species from the genera *Avena*, *Brachypodium*, *Bromus*, *Hordeum*, and *Lolium*. *Nassella pulchra* was recorded as exhibiting high cover in several stands but never was the dominant. Nonnative forbs included *Foeniculum vulgare*, *Hirschfeldia incana*, *Rumex crispus*, and *Vicia villosa*, among others. Native forbs included *Eschscholzia californica*, *Ranunculus californicus*, and *Sisyrinchium bellum*, among others. MCV = California Annual Grassland.

Native Bunchgrass Grassland (7) – Dominated by two species of native perennial bunchgrass species, either *Melica imperfecta* or *Nassella pulchra*. Other native grasses included *Nassella lepida*. Annual grasses included *Vulpia microstachys* and nonnatives typical of Valley and Southern Coastal Grassland. Forbs included *Bloomeria crocea*, *Calochortus clavatus* subsp. *clavatus* (List 4.3 - CNPS 2007), *Cryptantha clevelandii*, *Galium porrigens*, *Grindelia hirsutula*, *Layia platyglosa*, *Plantago erecta*, *Sisyrinchium bellum*, *Stachys bullata*, and *Trifolium willdenovii*. MCV = Purple Needlegrass (5); *Onion Grass (2).

***Yucca\Bunchgrass Scrub** (2) – Co-dominated by *Yucca whipplei* and *Nassella lepida*. In addition, soft-stemmed shrubs characteristic of Southern Coastal Scrub collectively contributed high cover, notably *Artemisia californica*, *Lotus scoparius*, and *Mimulus aurantiacus*. Forbs with the highest cover included *Chorizanthe palmeri*

(List 4.2 - CNPS 2007), *Eschscholzia californica*, *Plantago erecta*, *Selaginella bigelovii*, and *Stachys bullata*. Other grasses included *Melica imperfecta*, *Nassella pulchra*, and *Bromus madritensis*. MCV = *Chaparral Yucca\Purple Needlegrass.

Southern Coastal Scrub (17) – Dominated by soft-stemmed shrubs, including *Artemisia californica*, *Mimulus aurantiacus*, *Salvia mellifera*, or *Toxicodendron diversilobum*. One stand on the southwest corner of the study area near the core campus was dominated by non-native *Opuntia ficus-indica*. Other shrubs included *Baccharis pilularis*, *Hazardia squarrosa*, *Lotus scoparius*, *Lupinus albifrons*, and *Rhamnus crocea*. Forbs with the highest cover exhibited a vine or vine-like growth form, such as *Calystegia macrostegia*, *Galium californicum*, *Keckiella cordifolia*, and *Senecio mikanioides*. Other forbs included *Achillea millefolium*, *Carduus pycnocephalus*, *Conium maculatum*, *Gnaphalium californicum*, and *Salvia spathacea*, among others. Grasses with the highest cover were nonnative annuals typical of Valley and Southern Coastal Grassland, notably *Brachypodium distachyon*. MCV = California Sagebrush (6); *Sticky Monkey Flower (2); Black Sage (5); *Poison Oak (3); *Indian-Fig (1).

Chamisal Chaparral (1) – Dominated by *Adenostoma fasciculatum*. *Cercocarpus betuloides* and *Salvia mellifera* were also present. No forbs were found. Grasses with the highest cover were nonnative annuals typical of Valley and Southern Coastal Grassland. MCV = Chamise.

Mixed Chaparral (1) – Codominated by *Adenostoma fasciculatum* and *Cercocarpus betuloides*. *Rhamnus crocea* had the third highest shrub cover. One individual of *Arctostaphylos luciana* (List 1B.2 - CNPS 2007) was also found. Forbs with the highest cover were *Keckiella cordifolia*, *Salvia spathacea*, and *Symphoricarpos mollis*. Grasses with the highest cover were *Bromus diandrus*, *Leymus condensatus*, and *Nassella lepida*. MCV = *Birchleaf Mountain-Mahogany – Chamise.

Serpentine Chaparral (61) – Dominated by the strict serpentine endemic *Quercus durata* var. *durata* (Holland and Keil 1995; Safford et al. 2005). *Cercocarpus betuloides* and *Rhamnus crocea* were occasional, and *Garrya veatchii* was rare. Forbs with the highest cover were *Calystegia macrostegia*, *Galium californicum*, and *Stachys bullata*. Grasses with the highest cover were *Bromus diandrus*, *Bromus madritensis*, *Leymus condensatus*, *Melica imperfecta*, and *Nassella pulchra*. MCV = Leather Oak.

***California Bay\Leather Oak Mosaic** (1) – Codominated by *Umbellularia californica* and *Quercus durata* var. *durata*. *Quercus berberidifolia* and *Rhamnus crocea* had the second and third highest cover in this stand, respectively. Forbs and grasses with the highest cover were similar to those found in Serpentine Chaparral. This community exhibited a bi-modal physiognomy appearing as an equal and even mixture of an open-canopied, reduced form of Central and Southern Mixed Evergreen Forest (see Holland and Keil 1995) and Serpentine Chaparral. The California Bay\Leather Oak Mosaic was restricted to seeps on steep slopes in serpentine soils dominated by Yucca\Bunchgrass Scrub, and was therefore always mixed with *Yucca whipplei* in the understory or dripline. Only one stand exhibited discrete vegetation apart from the Yucca\Bunchgrass Scrub matrix. This community might be similar to the "Leather Oak-California Bay-*Rhamnus* spp. Mesic Serpentine NFD Super Alliance" found in Napa County by Thorne et al. (2004). MCV = *California Bay\Leather Oak.

***Toyon Woodland** (6) – Although toyon (*Heteromeles arbutifolia*) is commonly recorded as a shrub in California vegetation (Holland and Keil 1995), within this study area it exhibited both a shrub and tree form. *Heteromeles arbutifolia* trees were the dominant component of the Toyon Woodland. *Prunus illicifolia* had the second highest cover in this community and *Quercus agrifolia* and *Sambucus mexicana* were also important tree components. Shrubs with the highest cover included *Holodiscus discolor* and also species common to the study area's Southern Coastal Scrub. Forbs with the highest cover were *Carduus pycnocephalus*, *Stachys bullata*, and *Torilis arvensis*. Grasses with the highest cover included *Brachypodium distachyon*, *Leymus condensatus*, and *Melica imperfecta*. MCV = *Toyon.

Coast Live Oak Woodland (11) – Dominated by *Quercus agrifolia*. *Heteromeles arbutifolia* and *Umbellularia californica* were common trees with high cover. Shrubs with high cover included species common to the study area's Southern Coastal Scrub, notably *Toxicodendron diversilobum*. Forbs with high cover included *Carduus pycnocephalus*, *Galium porrigens*, *Salvia spathacea*, *Solidago californica*, and *Stachys bullata*. Grasses with high cover included *Elymus glaucus*, *Melica imperfecta* and nonnative grasses indicative of Valley and Southern Coastal Grassland. MCV = Coast Live Oak.

Valley and Foothill Riparian (11) – In the study area, ten Valley and Foothill Riparian stands exhibited a woodland physiognomy while one stand exhibited an open shrubland physiognomy. The ten Valley and Foothill Riparian woodlands were dominated by *Platanus racemosa*, *Q. agrifolia*, *Salix lasiolepis*, or *U. californica*. Other trees, such as *Salix laevigata* and *Heteromeles arbutifolia*, were occasional. *Baccharis pilularis*, *Rhamnus californica*, and *Toxicodendron diversilobum* had the highest shrub cover in these woodlands. Forbs with high cover included *Carex senta*, *Juncus patens*, *Helenium puberulum*, *Mimulus guttatus*, *Rorripa nasturtium-aquaticum*, and *Rumex crispus*. Grasses with the highest cover included *Agrostis viridis*, *Elymus glaucus*, *Phalaris aquatica*, *Piptatherum milliaceum*, and nonnative annuals indicative of Valley and Southern Coastal Grassland. The one shrub stand of Valley and Foothill Riparian was located adjacent to fenced-off cattle pasture on the western edge of the study area. It appeared that cattle had grazed this stand in the past based on numerous ruts found along the contours of sloped sections. The stand was dominated by *Baccharis pilularis* while *Ricinus communis* had the second-highest cover. *Typha latifolia* and a *Juncus* sp. had the highest forb cover, and *Lolium multiflorum* had the highest grass cover. MCV = California Sycamore (2); Coast Live Oak (2); Arroyo Willow (2); *Bay Laurel (4); *Coyote Bush (1).

Vegetation Map

Eleven plant community layers and an anthropogenic disturbance layer were created (Fig. 4). Total area mapped was 92.6 ha and was made up of 229 vegetation polygons. Anthropogenic areas covered about 3% (21 polygons) of the total area mapped and represented plantings, such as a Eucalyptus stand, and severely disturbed locales such as roads, irrigated pastures, and a small landfill/quarry. Anthropogenic coverage was excluded from all analyses. The three most extensive plant communities as a function of full extent areal coverage were, in descending order, Yucca\Bunchgrass Scrub, Native Bunchgrass Grassland, and Valley and Southern Coastal Grassland (Table 1). When ranking the three most extensive plant communities as a function of discrete areal coverage, the only change was that Valley and Foothill Riparian had more coverage than Valley and Southern Coastal Grassland. The three plant communities with the least full extent areal coverage were, in descending order, Chamisal Chaparral, Serpentine Chaparral, and Toyon Woodland. When ranking the plant communities with the least discrete areal coverage, the ranking became California Bay\Leather Oak Mosaic, Toyon Woodland, and then Serpentine Chaparral.

Serpentine Chaparral had the highest number of stands with discrete space, at 61, while California Bay\Leather Oak Mosaic, Chamisal Chaparral, and Mixed Chaparral were represented only by one stand with discrete area (Table 1). The largest mapped stand with discrete space was of Yucca\Bunchgrass Scrub, at 192,676 m^2, while the smallest stand mapped was of Serpentine Chaparral, at 9 m^2. Serpentine Chaparral also had the highest number of semi-stands at 45 while Chamisal Chaparral and Valley and Foothill Riparian had none. The largest semi-stand was of California Bay\Leather Oak Mosaic, at 13,680 m^2, while the smallest semi-stand was Yucca\Bunchgrass Scrub, at 4 m^2.

Ecotone Analysis

Out of the 89.9 ha of mapped vegetation (not including anthropogenic cover), 54.8 ha (61%) was discrete, non-overlapping vegetation, and 35.1 ha (39%) was overlap (ecotone plus semi-stand). When all semi-stands were removed and the analyses repeated, the study area was found to have 32.5 ha (36%) of ecotone (Fig. 5). Of all vegetation coverages, Yucca\Bunchgrass Scrub and Native Bunchgrass Grassland occupied the largest total area (discrete plus overlap) and discrete coverage, respectively. The plant community with the highest amount of ecotone (176,399 m^2) and highest amount of total overlap (179,942 m^2) was Native Bunchgrass Grassland.

Only Chamisal Chaparral, Valley and Foothill Riparian, and Yucca\Bunchgrass Scrub exhibited discrete areal coverages more than 50% of their respective total areas (Fig. 6). The other eight plant communities had more of their area represented as ecotone than as discrete areal coverage. Thus, in general, a greater percentage of each community's full extent areal coverage was ecotonal, even though the majority of the study area was discrete space.

Finally, each plant community's ecotone and total overlap were analyzed to determine which other communities contributed or shared the majority of that area (Table 2). Southern Coastal Scrub was found to have the greatest areal contribution with the most number of plant communities. Valley and Southern Coastal Grasslands had the second greatest areal contribution to both ecotone and total overlap space with the most plant communities.

Among the 79 semi-stands, 51.9% were found within Yucca\Bunchgrass Scrub, 22.1% within Native Bunchgrass Grassland, 20.2% within Valley and Southern Coastal Grassland, 2.9% within Southern Coastal Scrub, 1.9% within Valley and Foothill Riparian, and 1.0% within Mixed Chaparral. All of the semi-stands in Yucca\Bunchgrass Scrub and Native Bunchgrass Grassland were on serpentine soil based on the overlay of a soils map (Ernstrom 1984). On non-serpentine soils, semi-stands were relatively less common but they were most often found in a matrix of Valley and Southern Coastal Grassland, then Southern Coastal Scrub.

Discussion

Vegetation Classification

Based on the Holland and Keil classification scheme, 11 visually distinct plant communities were mapped. If a more detailed classification

FIG. 4. Composite vegetation map of study area depicting eleven plant communities and an anthropogenic disturbance coverage. V.S.C.G. – Valley and Southern Coastal Grassland; N.B.G. – Native Bunchgrass Grassland; Y.B.S. – Yucca\Bunchgrass Scrub; S.C.S. – Southern Coastal Scrub; C.C. – Chamisal Chaparral; M.C. – Mixed Chaparral; S.C. – Serpentine Chaparral; C.B.L.O. – California Bay\Leather Oak Mosaic; T.W. – Toyon Woodland; C.L.O.W. – Coast Live Oak Woodland; V.F.R. – Valley and Foothill Riparian.

TABLE 1. SPATIAL CHARACTERISTICS OF THE STUDY AREA'S PLANT COMMUNITIES. Total area represents full extent and semi-stand polygons collectively.

Plant Community	Total Area				Full Extent	Semi-Stands
	Area (ha)	% study area	Rank order	# of polygons	# of polygons	# of polygons
Valley and Southern Coastal Grassland	24.8	27.6	3	14	11	3
Native Bunchgrass Grassland	28.1	31.3	2	9	7	2
Yucca\Bunchgrass Scrub	30.3	33.7	1	20	2	18
Southern Coastal Scrub	16.1	17.9	4	20	17	3
Chamisal Chaparral	0.9	1	11	1	1	0
Mixed Chaparral	3	3.4	8	2	1	1
Serpentine Chaparral	1.8	2	10	106	61	45
California Bay\Leather Oak Mosaic	3.5	3.9	7	4	1	3
Toyon Woodland	2.2	2.5	9	9	6	3
Coast Live Oak Woodland	7.4	8.2	6	12	11	1
Valley and Foothill Riparian	9.4	10.5	5	11	11	0

scheme, such as MCV, had been applied, then several more vegetation types would have resulted from the split of Native Bunchgrass Grassland, Southern Coastal Scrub, and Valley and Foothill Riparian communities, as noted in the results. Because the vegetation of the study area has been mapped at a fine scale and lists of the three most dominant tree, shrub, forb, and grass species are

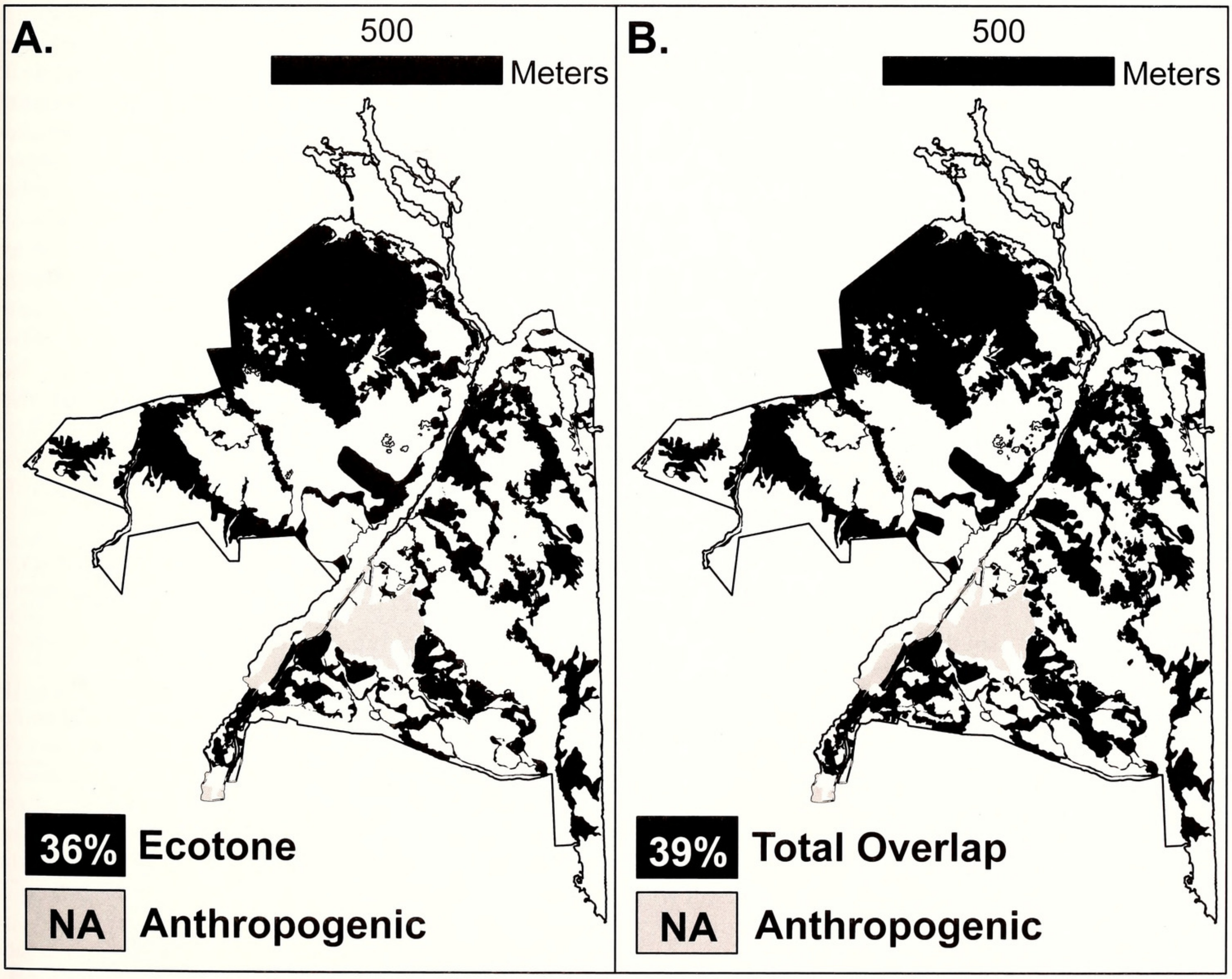

FIG. 5. Ecotone and total overlap as percentages of study area. Anthropogenic area is depicted as gray coverage and was not included in any areal analyses. A. 36% of study area is ecotonal space. B. 39% of study area is total overlap.

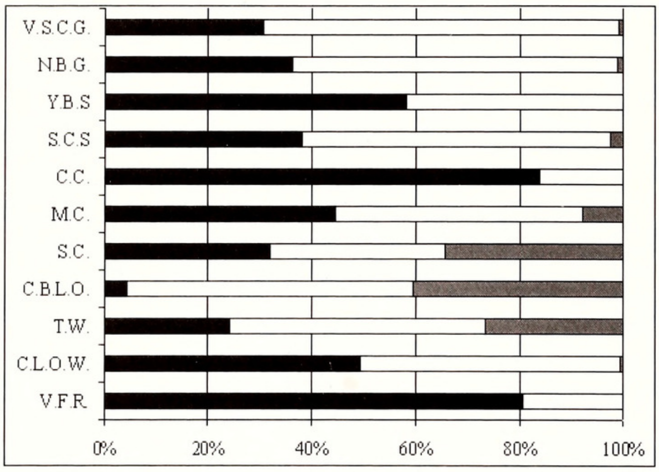

FIG. 6. Percent of each plant community's total area (see Table 1) that is discrete (black), ecotone (white), and semi-stand (grey). For example, 30.6% of all V.S.C.G. mapped area is discrete, 68.5% is ecotone, and 0.9% is semi-stand. See Fig. 4 for abbreviation meanings.

linked relationally to polygons in the GIS, a more detailed classification scheme with greater resolution could be applied in the future. However, crosswalking to a classification scheme with finer hierarchical detail, specifically the association level in the CNDDB (2003), may not be possible for all plant communities of the study area without further quantitative cover estimates.

There are potentially many undescribed vegetation types in California. Three out of the eleven plant communities found in the study area were previously undescribed. Another recent classification and mapping effort (Thorne et al. 2004) also documented a high proportion (54%) of undescribed communities. California has the greatest vegetation type diversity in the nation (Sawyer and Keeler-Wolf 1995) and much work remains to classify its vegetation, which is an important goal for conservation (Margules and Pressey 2000). In addition, serpentine soils are known to harbor unique plant species and communities (Kruckeberg 1992, 1999; Harrison et al. 2000) and further work to classify vegetation types associated with this substrate may be especially fruitful and beneficial to conservation.

Vegetation Map

In vegetation mapping, the purpose (e.g., regional planning, forestry, etc.), spatial extent of the vegetation (Küchler 1953; Küchler 1988b; Franklin and Woodcock 1997; Stohlgren et al. 1997), and mapping technique (Thorne et al. 2004) influence the resolution and accuracy of the map. Although accurate regional vegetation maps have been created using remote sensing techniques (Driese et al. 2004; Hong et al. 2004; Thorne et al. 2004), the delineation of boundaries between communities can be challenging because soil surface reflectance can influence signal properties (Abeyta and Franklin 1998), similar spectral signatures between adjacent patches can result in misclassification or incorrect stand delineation (Goodchild 1994), and transitions don't always represent multiple-class membership of pixels (Schmidtlein and Sassin 2004). Because of these problems, higher resolution imagery or boundary ground-truthing (Abeyta and Franklin 1998) are needed to improve boundary delineation in regional maps. For local scale maps, stands can be mapped that are too small to be detected with remote sensed technology (Miyamoto et al. 2004). It is also at the local scale that ecotones may be most conspicuous and difficult to ignore. Therefore, adopting the method presented herein or by Miyamoto et al. 2004 (used for sharp wetland boundaries) may be advantageous when depicting vegetation at the local scale.

To our knowledge, this is the first vegetation map that depicts plant communities by their full

TABLE 2. THE MOST OVERLAPPING VEGETATION TYPE (MOV) AS A PERCENT OF EACH PLANT COMMUNITY'S ECOTONE AND TOTAL OVERLAP AREAS. The MOV remained the same for every plant community for both ecotone and total overlap areas. N.B.G – Native Bunchgrass Grassland; V.S.C.G. – Valley and Southern Coastal Grassland; S.C.S. – Southern Coastal Scrub; Y.B.S. – Yucca\Bunchgrass Scrub. For example, N.B.G. occupied 68.8% of V.S.C.G. total ecotone space, and 67.8% of V.S.C.G. total overlap space.

Plant Community	Most Overlaping Veg. Type (MOV)	MOV as % of Ecotone	MOV as % of Total Overlap
Valley and Southern Coastal Grassland	N.B.G.	68.8	67.8
Native Bunchgrass Grassland	V.S.C.G.	64.7	65.4
Yucca\Bunchgrass Scrub	N.B.G.	51.5	47.4
Southern Coastal Scrub	V.S.C.G.	44	45
Chamisal Chaparral	S.C.S.	90.3	90.3
Mixed Chaparral	S.C.S.	82.5	67.8
Serpentine Chaparral	Y.B.S.	92.9	96.5
California Bay\Leather Oak Mosaic	Y.B.S.	90.5	90.5
Toyon Woodland	S.C.S.	54.7	45
Coast Live Oak Woodland	S.C.S.	43.4	41.4
Valley and Foothill Riparian	V.S.C.G.	50.7	50.9

extent in a multi-layered approach, thus also representing ecotonal space. In this map, the lack of artificial boundaries between communities may result in a more precise vegetation map than contemporary mapping techniques implemented at a similar scale. However, this ground-based method of vegetation mapping might not always be feasible or appropriate for other mapping efforts. Regardless of the methods utilized in future vegetation maps, we think they can be greatly improved upon by accounting for ecotonal space and clearly stating how mapping unit boundaries are defined.

Ecotone Analysis

The mixture of different soil types, together with the diverse topography, resulted in a number of plant communities with a heterogeneous distribution and structure across a small landscape. These factors also contributed to the equally varied distribution, structure, and extent of ecotones in the study area. In general, communities with many stands and large total areal coverage were found to have the highest amount of ecotone with other plant communities as a percent of the study area, except for Valley and Foothill Riparian vegetation. Not surprisingly, the sharpest boundaries or narrowest ecotones were between hydrophytic and adjacent upland communities (Walker et al. 2003).

In the field, plant community boundaries also appeared to be strongly associated with sharp or gradual transitions between soil types, although transitional areas were not depicted on the 1:24,000 scale soil map (Ernstrom 1984). Other factors, such as succession and biological invasions may also be important. Southern Coastal Scrub, which had high overlap with other communities, can be seral in this region (Callaway and Davis 1998) and Valley and Southern Coastal Grassland, which also exhibited high ecotonal overlap with multiple communities, is dominated by invasive grasses (D'Antonio and Vitousek 1992; Seabloom et al. 2003). If nonnative grasses become more successful through disturbance (Stylinski and Allen 1999; Keeley et al. 2005), adaptation to serpentine soils (Harrison et al. 2001), air pollution (Huenneke et al. 1990; Weiss 1999; Fenn et al. 2003), or possibly climate change (Dukes and Mooney 1999), then ecotone space resulting from invasion fronts (Hoffman et al. 2004) could greatly increase since much of the study area is surrounded by Valley and Southern Coastal Grassland.

The large proportion of semi-stands that occurred on serpentine soils most likely reflects the high amount of seeps and springs that are associated with this substrate (Kruckeberg 1984). Most of the serpentine soil was covered in Yucca\Bunchgrass Scrub and Native Bunchgrass Grassland, which served as the matrix communities for the majority of semi-stands. The semi-stands found within these vegetation types appeared to be highly associated with seeps and were approaching larger structural physiognomies compared to matrix communities, such as shrubland (e.g., Serpentine Chaparral), or a combination of shrubland and woodland (e.g., California Bay\Leather Oak Mosaic). Hydrology is important in structuring serpentine vegetation and ecotones (Tolman 2006), and if it were not for the large number of seeps at the study site, semi-stands probably would not have been as common. In addition, it is likely that seeps with a greater amount of available water provided the conditions necessary for discrete Serpentine Chaparral to form, reflected by their large number of small sized stands (Fig. 4). Semi-stands were most abundant within serpentine substrate, but in general, were a small component of the study area (Fig. 5).

While mapping vegetation as described above portrays the areal extent of ecotone between adjacent stands, such mapping does not reveal the specific composition of the ecotone. Ecotones can consist of more individuals or areal cover of one community type than of the other, and/or include unique species. The methodology presented herein will provide the areal extent of the ecotone, but additional observations within the ecotone must be performed if detailed species composition, vegetation structure, or vegetation classification are important.

Conclusion

In Poly Canyon, plant communities form a multi-layer mosaic of stands that vary in shape and size over the landscape. These communities overlap and integrate forming relatively gradual to discrete ecotones. The major advantage of mapping vegetation to its fullest extent, as described herein, is to obtain a more accurate and precise representation of plant community organization. Furthermore, community classification and stand boundary delineation is also accurate because the data is derived directly from ground-based observations, rather than through remote sensing (e.g., Hulbert and French 2001). This method may also be useful in documenting change in plant community boundaries because the ecotonal areas mapped by this method may be the most dynamic portion of the landscape (Risser 1995).

While ecotones are often studied to understand environmental gradients and natural processes, the actual portrayal of ecotones on vegetation maps has been neglected. It is therefore noteworthy that about one third of the vegetation in this study was ecotonal and that the majority of plant communities exhibited a higher proportion of their total area as ecotone rather than discrete space. These findings suggest that, in some instances, vegetation maps created with artificial community boundaries may misrepresent a large portion of the mapped area. This misrepresentation results from forcing single-layer canopy coverage on complex vegetation mosaics, such as those found on the central coast of California.

Although a significant proportion of the study area was found to be ecotonal space, this finding may not be representative of nearby sites with similar area or central coast vegetation at different scales. This ground-based approach may also not be suitable for the depiction of vegetation greater than the local scale, although the concept of mapping stands of vegetation to their full extent in order to capture ecotonal space could be incorporated into regional mapping methodology. An understanding of the characteristics and amount of ecotonal space at multiple scales would be beneficial and an important direction for future research. As this study has shown, ecotones can comprise a large portion of the landscape. Furthermore, ecotones can be areas with high species diversity (Risser 1995), and they may be the most responsive landscape unit to climate change (Kark and van Rensburg 2006) and an important source of evolutionary novelty (Smith et al. 1997). Inclusion of ecotones in vegetation maps would result in more realistic depictions and could increase usefulness towards conservation efforts.

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