

VEGETATION PATTERNS IN THE MEDITERRANEAN-DESERT ECOTONE OF BAJA CALIFORNIA, MEXICO

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ABSTRACT

The Pacific coast of NW Baja California is a hotbed of plant species richness and endemism. Greater San Quintín (GSQ), Baja California, Mexico, is located near the southernmost reaches of the California Floristic Province in a vegetation transition zone. Perennial species distributions were recorded and used to assess the distribution and richness of rare, narrowly endemic and native taxa. A Principal Components Analysis assessed the major elements in the perennial flora, and separated the habitats to indicate the primary factors affecting plant distributions. Distribution of plant species is related to elevation and soil type. The data analysis identifies three distinct areas of species richness, each on a different substrate. Three major habitats were resolved in the analysis; however, indicator species provide greater resolution of habitats with similar soils. Range size on a regional scale was not related to local abundance of perennial species. Across the landscape, native, rare and endemic species richness patterns are very similar, suggesting that native plant richness can be used as a proxy for identifying areas rich in sensitive species. This method provides useful data to conservation efforts. Coastal habitat is essential for many species and conservation recommendations for the region are detailed.

RESUMEN

La costa pacífica del noroeste de Baja California es un foco de riqueza y endemismo para numerosas especies vegetales. La región de San Quintín, Baja California, México, se localiza cerca de los límites australes de la Provincia Florística de California, en una zona de vegetación de transición. Se registró la distribución de especies perennes para evaluar la riqueza y distribución de taxa nativos raros y de endemismos restringidos. Un Análisis de Componentes Principales evaluó los elementos primordiales en la flora perenne y separó los hábitats para indicar factores primarios que afectan la distribución de la vegetación. La distribución de las plantas está relacionada con la elevación y el tipo de suelo. El análisis de datos identifica la riqueza de especies vegetales en tres distintas áreas, cada una en un sustrato diferente. Se determinaron tres hábitats principales en el análisis; sin embargo, las especies indicadoras aportan mayor resolución de hábitats con suelos similares. El tamaño del rango a escala regional no tuvo relación con la abundancia local de especies perennes. A través del paisaje, los patrones de riqueza de especies nativas, raras y endémicas son muy similares, sugiriendo que la riqueza de flora nativa puede ser utilizada como un agente para identificar áreas ricas en especies sensibles.

KEY WORDS: Endemism, mapping, maritime succulent scrub, rarity, species richness, San Quintín, Baja California, vernal pools

INTRODUCTION

Around the mid-latitude belt of the globe, the western side of continents is occupied by deserts while the eastern side is normally covered by forests. This distribution of coastal drylands is driven by the global circulation of oceans: Equator-bound currents on the eastern side of large oceans are deflected westwards by the rotational force of the Earth, to form the equatorial currents and the easterly trade winds. As the westbound surface waters move away from the continents, they pull cold, nutrient-rich waters to the surface that generate a cool, stable coastal atmosphere, with little evaporation from the sea and very low rainfall other than morning fogs. In coasts neighboring these oceanic upwellings, typical coastal fog deserts tend to develop, forming some of the driest ecosystems on earth. Thus, the large-scale circulation of the ocean is the main reason why

coastal deserts are always found on the west side of continents, such as the Succulent Karoo in Africa, Atacama in Chile, the Atlantic Coastal Desert of Morocco, or the deserts of Baja California. All these fog-driven drylands are adjacent to winter-rain Mediterranean ecosystems in higher latitudes, and large coastal Mediterranean-to-desert ecotones driven by fog, more than rains, occupy the transition areas along these coasts (Ezcurra & Mellink 2013).

The over-arching pattern of global species diversity is of increased species numbers and decreased range sizes toward the equator (Rapoport's rule, Stevens 1989). However, regions of very high species diversity and endemism are also found in areas of Mediterranean climate at intermediate latitudes. The California Floristic Province (CFP) has been designated as a global biodiversity hotspot, moreover an area of high endemism that has been heavily impacted by human activity (Myers et al. 2000). The geographic distribution of the California Floristic Province (CFP) essentially coincides with the presence of winter-spring rainfall and the absence of summer precipitation (Minnich & Franco-Vizcaino 1998; Caso et al. 2007).

At the southern extreme of the CFP, the desert-to-Mediterranean transition in northwestern Baja California has a large proportion (~10%) of endemism, including 172 locally endemic species, many of which are micro-endemic to areas of less than 50 hectares (O'Brien et al., in press). Little is known about the factors controlling the distributions of these narrowly endemic species in these ecotonal drylands.

As we enter a period of accelerated global environmental change, it is predicted that we will see extinctions on an unprecedented scale (Thomas et al. 2004). The CFP is no exception and current estimates are that 66% of endemic species will experience up to 80% range reductions in the next century under even conservative climate change scenarios (Loarie et al. 2008). However, the impacts of climate change have been difficult to assess due to the absence of baseline data from which we can establish distribution patterns and assess the fate of rare and endemic taxa (Jansson 2009).

The southern limit of the CFP has been the subject of debate for decades. Rather than a sharp boundary, there is a gradual Mediterranean-scrub-to-desert transition that begins near the U.S./Mexico border and ends near the 30th parallel near El Rosario according to Shreve (1936). This transitional zone has the greatest floristic diversity in the state of Baja California and transitional vegetation associations recorded here have the highest endemic community values (i.e., greatest densities of narrowly endemic taxa, Peinado et al. 1995a). In the present study we focus on the area between parallels 30 and 31 on the Pacific Coast of Baja California, Mexico, here referred to as 'Greater San Quintín' (GSQ; Fig. 1). Although rainfall is low for most of the year, with an annual average of 105–137 mm (Vanderplank 2011), San Quintín experiences frequent heavy fogs caused by the cool upwelling of the California current off-shore (Herbert et al. 2001), and the associated humidity provides significant extra water resources, to which the local vegetation is adapted (Rundel et al. 1972).

The ecotonal position of San Quintín (where the Mediterranean CFP transitions into the Sonoran desert to the south) often makes species distributions patchy and discontinuous, with the vegetation being very heterogeneous in this region (Vanderplank 2013). Greater San Quintín lies at the southern end of this transitional vegetation and is home to sixty-seven taxa that are endemic or near-endemic to NW Baja California (Vanderplank 2011). The unusual mix of CFP species with plants from the desert area to the south make GSQ a floristically rich area with 433 taxa documented in recent years (Vanderplank 2011). Thirty-four percent of the species that comprise the flora of GSQ are rare and/or locally endemic, making GSQ a priority region for conservation (Vanderplank 2011).

Greater San Quintín is currently under consideration for declaration as a natural protected area or *Área Natural Protegida* (ANP) under Mexican law. Local conservation organizations have identified four distinct terrestrial habitats in need of conservation in GSQ: salt marsh, dunes and beaches, rivers and riparian areas, and the maritime succulent scrub (note that "riparian" areas in this region are most often dry washes with sandy substrates). The habitats have been similarly categorized by the *Instituto Nacional de Estadística Geografía e Informática, México* (INEGI), although upper salt flats are distinguished from inundated marshes.

Conservation efforts are unavoidably biased by available biodiversity data. The challenge of identifying core areas for conservation given the rich assemblage of rare and endemic plants in GSQ is heightened by

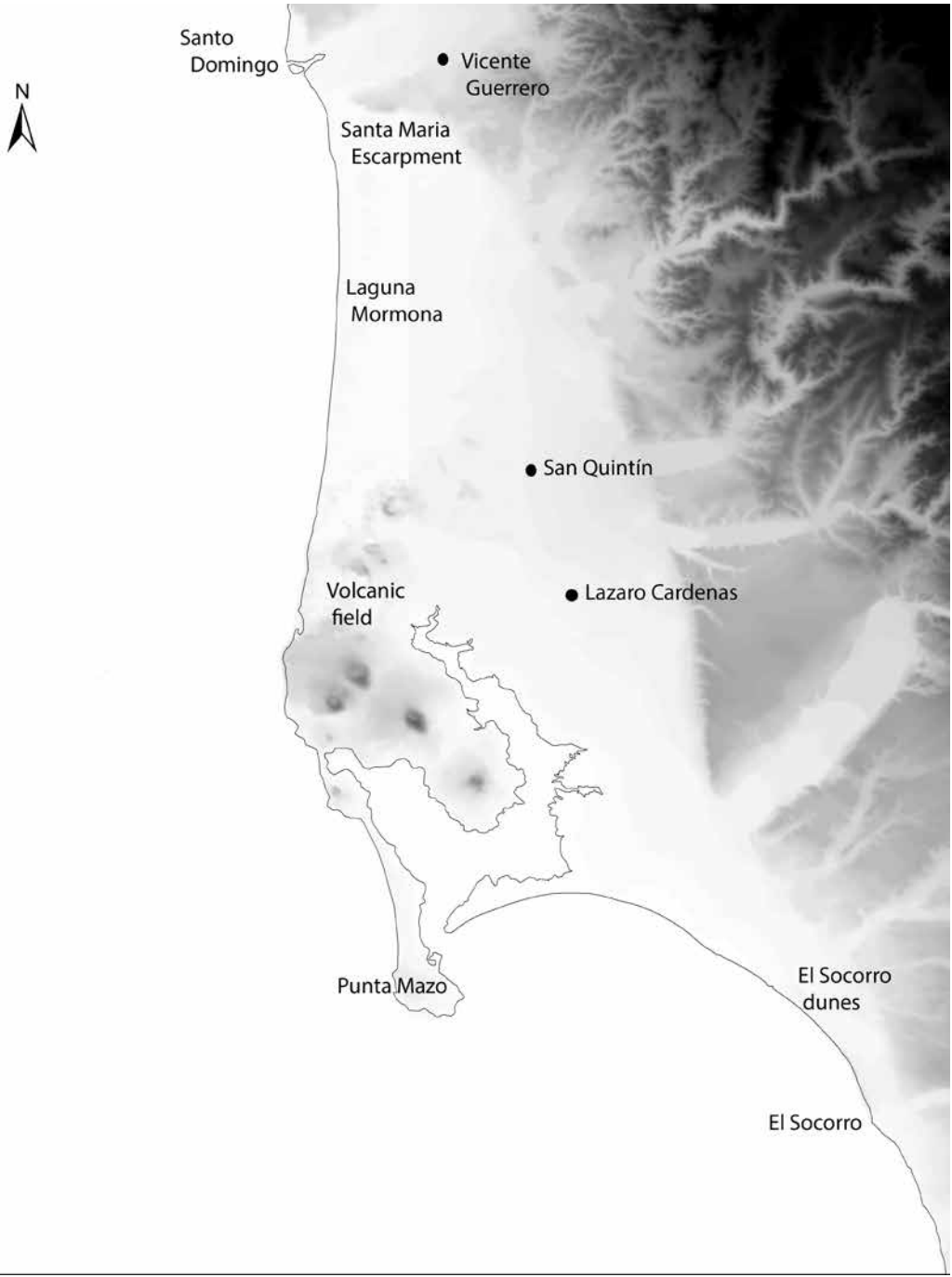


Fig. 1. Topography and local place names within Greater San Quintin. N 30.18–30.45 and W 115.48–116.03.

competition for land use and the heterogeneity of the vegetation itself. Despite the very limited global extent of the maritime succulent scrub (Cartron et al. 2005), the saltmarsh habitat is most frequently the primary conservation target in this region. The saltmarshes of GSQ provide a suite of ecosystem services and provide a model system for restorations in other areas along the Pacific coast (West 2000) yet are the most floristically depauperate habitat, and harbors only one endemic taxon (Bell 2010; Vanderplank 2011).

Fine-scale phytosociological studies in this region have shown diverse shrub associations in northwestern Baja California, where the climate gradient from north to south correlates with increased floristic diversity (both for endemic species and diversity of life-forms) as aridity increases (Peinado et al. 1995a, 1995b). This is the first study conducted at a macroecological scale in this region ($1 \times 1 \text{ km}^2$) and brings new perspective on the larger factors controlling vegetation distributions in this region.

A goal of this study was to investigate the distribution of the long-lived taxa that dominate the vegetation and can be identified year-round. This study determines the current status of the terrestrial perennial vegetation and provides baseline data from which future changes in the flora can be assessed and monitored. We here try to assess which factors are dominant in the distribution of vegetation, and in particular, in the distribution of rare and endemic species.

MATERIALS AND METHODS

Sampling methods.—A one-km grid of cells was created in ESRI ArcMap and georeferenced to overlay the study area (the top-left NW corner of the grid lies at N 30.738 and W 116.039). Each grid cell became the macroecological sampling unit for the terrestrial vegetation. TerraSync software was used with a Trimble Juno GPS unit in the field. Grid cells that contained only agricultural fields or urbanized areas, as well as cells with less than 10% cover of natural vegetation were excluded from the analysis.

Quantitative data on presence and abundance of perennial species and selected invasive annual species was gathered within each grid square (the estimation method is described below). All perennial plants that could be identified year-round were included in the analyses; geophytes and herbaceous perennials that could not be consistently identified throughout the year were excluded. Non-native annual taxa that were selected for inclusion were abundant, identifiable year-round, and judged to be potentially invasive. The goal here was to provide spatial information on the current extent of the most abundant non-native species. This study follows the vascular plant checklist for Baja California (Rebman in review) for taxonomy and nativity.

Each square km that had native vegetation was visited to assess a number of traits of the vegetation. A visual assessment was made to estimate the percent natural vegetation and to determine species present. Trials showed that this method encountered a significantly higher number of species than alternative methods (e.g., quadrats or transects) that subsample smaller areas. Several taxa cannot readily be differentiated from one another at all times of the year, these were pooled at a taxonomic level higher than species. For example, the three species of the genus *Lycium* reported from the San Quintin area (these drought-deciduous shrubs cannot easily be distinguished without leaves). Admittedly less than ideal, this approach was preferred over omitting these taxa from the study (see supplemental information table for taxon list).

Abundance per km cell was estimated using the method of Nichols (1930) and the following categories of abundance: (1) rare: fewer than 3 individuals encountered; (2) scarce: 3–10 individuals; (3) uncommon: >10 but < 100 individuals ($1/10,000 \text{ m}^2$); (4) frequent: 100–1,000 individuals ($1/1,000 \text{ m}^2$); (5) common: 1,000–10,000 individuals ($1/100 \text{ m}^2$); (6) abundant: 10,000–100,000 individuals ($1/10 \text{ m}^2$); and (7) dominant: >100,000 individuals ($1/1 \text{ m}^2$). Estimates were based on number of plants seen and their distribution patterns. When estimating numbers of plants that sprout from roots or rhizomes (e.g., salt grasses such as *Distichlis* spp.), the numbers of individual sprouts were considered, such that these should not be taken to estimate numbers of genetic individuals.

Analysis.—The resulting data matrix for each cell listed perennial and selected non-native annual taxa scored for presence/absence. Perennial species richness was calculated for each square. Pearson's residuals (the standardized difference between the observed species richness in each grid square and the mean over all squares,

Everitt 1992) were calculated. Because Pearson residuals are distributed as normal deviates, those squares that departed significantly ($P < 0.01$) from the mean richness were identified (Everitt 1992) to show areas of significantly high or low richness.

Each taxon was classified according to (1) its origin (native/non-native), (2) endemism (endemic/non-endemic), (3) regional rarity, and (4) local rarity or abundance. All taxa that are restricted to the Baja California peninsula (most of which are also endemic, or nearly so, to the CFP within the peninsula) were classified as endemic. For rarity we followed O'Brien et al. (in press), which is based on previous work by the California Native Plant Society: taxa on any of three lists of concern (i.e., rare globally, rare in CFP Baja California but more common elsewhere, and watch-list taxa) were together categorized as "rare" for our analysis (in the few incidences where multiple taxa were lumped, the category of the most abundant taxon was used). Data on abundance or rarity within Greater San Quintín were drawn from the vegetation data. Species found in more than 40 one-km cells were classified as locally abundant, species found in less than 10 one-km cells were classified as locally scarce, and all species between the two thresholds were classified as intermediate. We tested for association between regional and local rarity, using X^2 contingency-table analysis.

ESRI ArcMap was used to map species distributions across the study area. Data from the matrix were attached to the grid layer using spatial coordinates for each cell. Relevant data layers were obtained from the Instituto Nacional de Estadística y Geografía, México (INEGI 1997, including shore outline, elevation, relief, soil, and habitat types). Following analysis of the data matrix, squares with extreme species richness or paucity (Pearson's residuals, $P < 0.01$) were mapped. The same was done for species richness for three subsets of taxa: native, endemic, and rare species.

Multivariate analysis.—To examine the distribution of species across habitat types as distinguished by The Nature Conservancy of Baja California, a non-standardized principal components analysis (PCA) of the presence-absence matrix for 163 native perennial taxa was conducted. Because the cross-product of two species vectors with presence-absence is simply the number of sites shared by both species, and, reciprocally, the cross-product of two presence-absence site vectors is the number of shared species, PCA on presence-absence data will reflect the number of co-occurrences as a measure of ecological similarity (Ezcurra 1987). The resulting PCA axes were tested for significance using the broken-stick model (Jackson 1993). These scores were then mapped to extract the dominant habitat type for each km square in the analysis. This map was compared to the habitat maps from INEGI and habitat maps generated using indicator species. An indicator species from each of the primary habitats was selected based on observed consistent presence in, and restriction to, specific habitat.

RESULTS

Vegetation patterns.—The analysis of vegetation tallied a total of 163 taxa, including 140 native perennials, across the 206 one-km cells (Table 1). This analysis allowed individual taxa to be mapped across the study area and their abundance displayed for each km square. The abundance distribution of endemic and rare species did not differ significantly from that of the total native flora within the Greater San Quintín area ($X^2 = 1.86$; $df = 2$, $P = 0.39$; Table 1), indicating that plants that are rare at a regional scale may be locally abundant within our study site, and, conversely, that plants that are regionally common may be locally scarce within our site.

Total species richness within each one-km cell varies across the study region (Fig. 2). The spatial distribution of significantly ($P > 0.01$) high and low Pearson's residuals for the whole flora shows some well-defined patterns (Fig 3a), especially for high-diversity cells, that tend to occur in three distinct spatial clusters. These spatial patterns of high richness are repeated in a similar manner for subsets of the flora (total native, Fig. 3b; endemic, Fig. 3c; rare taxa, Fig. 3d).

Species richness is low adjacent to agriculture and urbanized areas (compare Fig. 3 to Fig. 5b). Richness in the salt marshes and saline flats is much lower than in other habitats. This is particularly evident north of the volcanic field and south of the Santa María Escarpment in the area surrounding Laguna Mormona (note bands of pale yellow squares along the coast; Fig. 3a & b). Non-native taxa are especially rich in riparian areas,

TABLE 1. Native species total (140 species) and parsed into two categories of regional rarity within the CFP in Baja California (endemism and rarity), and by their local abundance category based on their frequency within Greater San Quintín (scarce, intermediate, or abundant).

Local Rarity	Endemic	Rare	Total native
Scarce	12	16	67
Intermediate	12	16	47
Abundant	5	8	26
Totals	29	40	140

and their distributions follow all major drainages. The non-native iceplant *Mesembryanthemum crystallinum* occurs almost ubiquitously across the study area. It is interesting to note that there was no correlation between percent natural vegetation in a square and species richness ($r = 0.11$, $df = 196$; $P = 0.13$). This absence of a clear species-area relationship at the one-km cell scale is most likely due to heterogeneity of the landscape; three habitat types coexist in a fraction of a one-km cell in whereas in others an entire km cell of degraded salt marsh that might have only four perennial species.

Areas of high species richness.—Three primary regions of high species richness emerge from the vegetation study: at the northern and southern extremes of the study area and along the coast adjacent to the volcanic field.

Northern biodiversity hotspot: The northern region of high species richness has two distinct subareas: Santo Domingo wash (northern boundary of the study area) and a clay mesa (slightly southeast from the wash). The Santo Domingo wash shows high species richness when all taxa are considered (Fig. 3a); however, richness here decreases somewhat when non-native taxa are excluded (Fig. 3b), and the area has few rare (Fig. 3d) or endemic (Fig. 3c) species. In contrast, the clay mesa in Colonia Vicente Guerrero, north of the Santa Maria escarpment, presents a strong signal of high species richness for native, endemic, and rare species (i.e., compare Figs. 3a–d). This area is a disturbed patch of vegetation with diverse succulent scrub and some small remnant-but-degraded vernal pools. Like the Santo Domingo wash this area has significantly more non-native species than typical of the study area as a whole.

Volcanic coast hotspot: The coastal strip near the volcanic field that includes the tip of the sandy peninsula at Monte Mazo is particularly diverse. This area includes a complex patchwork of habitats along the coast which likely contributes to high species richness. The precise cells that show significant richness among the analyses vary slightly (i.e., compare Figs. 3a–d), but the coastal strip is always rich in native, rare, and endemic species. There are not significantly high numbers of non-natives in this area (consistent with the relatively intact nature of the habitats).

Southern dunes hotspot: Near the southern end of the study area, the El Socorro Dunes stand out as the largest area of high species richness. Because only one habitat type is represented across several cells here, the observed high richness is not the result of habitat heterogeneity. Although there are some differences in the pattern of cells that harbor significantly high numbers of native, endemic, and rare taxa, the area is rich in all of these.

Multivariate analysis.—The Principal Components Analysis showed two axes that, according to the broken stick test, departed significantly from a random model (Fig. 4). The first axis is positively correlated with topographic elevation ($r = 0.41$, $df = 204$, $P < 0.0001$) and displays a salinity-elevation gradient: plants of coastal habitats are on the left and those of maritime succulent scrub are on the right (positive on axis 1). The second axis reflects soil type on coastal habitats and separates saltmarshes (positive on axis 2) from freshwater and sand dune species (negative on axis 2). The corresponding species plot, accordingly, shows three distinct clusters of species dominating in three habitat types: (a) scrub, (b) saltmarshes, and (c) sandy soil plants regardless of whether on dunes or in riparian areas (Fig. 4). When mapped back onto the study area, the three habitats identified by the PCA bi-plots produced a map that was very consistent with the vegetation chart (INEGI 1997 produced with completely different methods (Fig. 5).

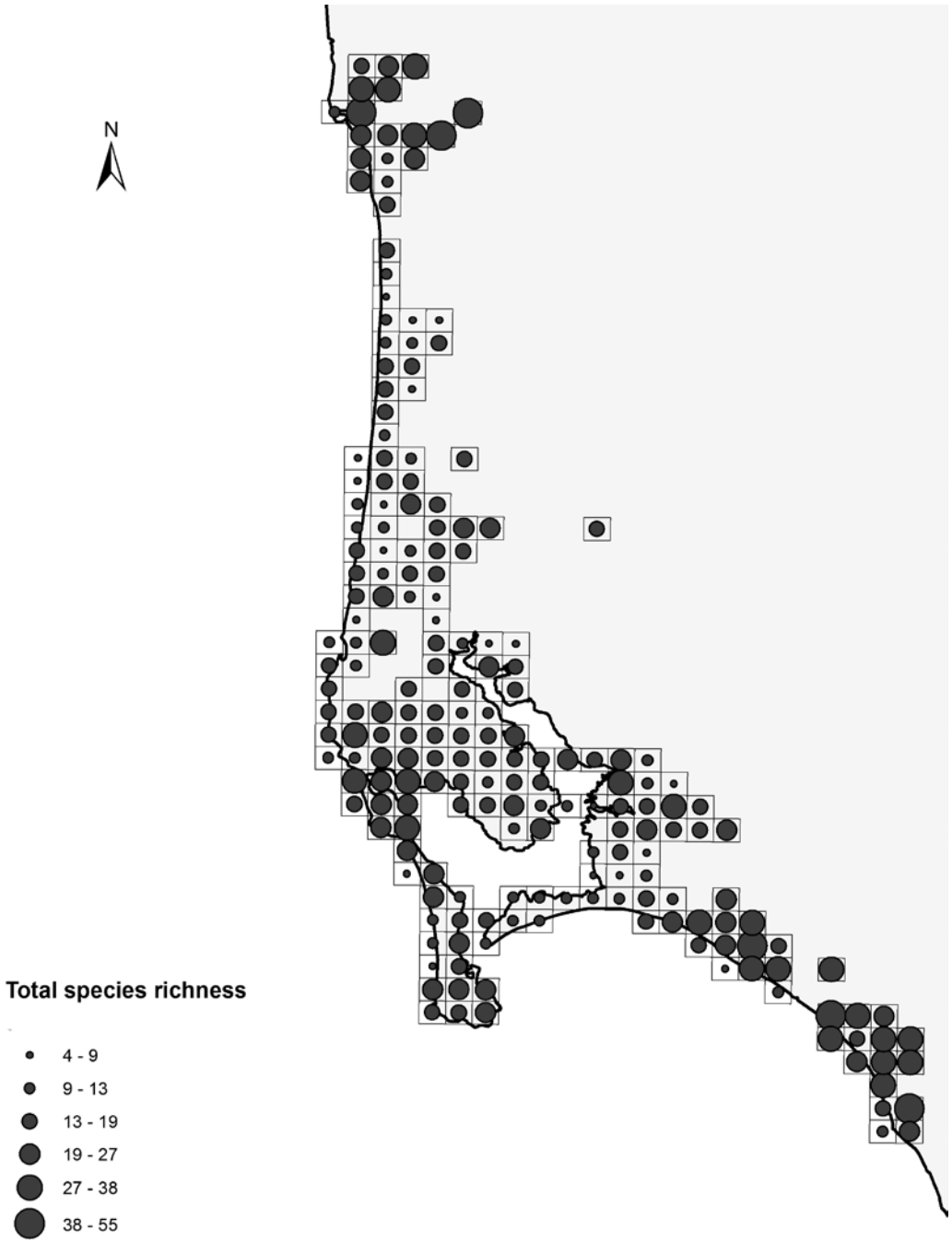


FIG. 2. Total species richness in 206 one-km cells for perennial vegetation of Greater San Quintin. As indicated at lower left, the size of the circle reflects number of species recorded in each cell.

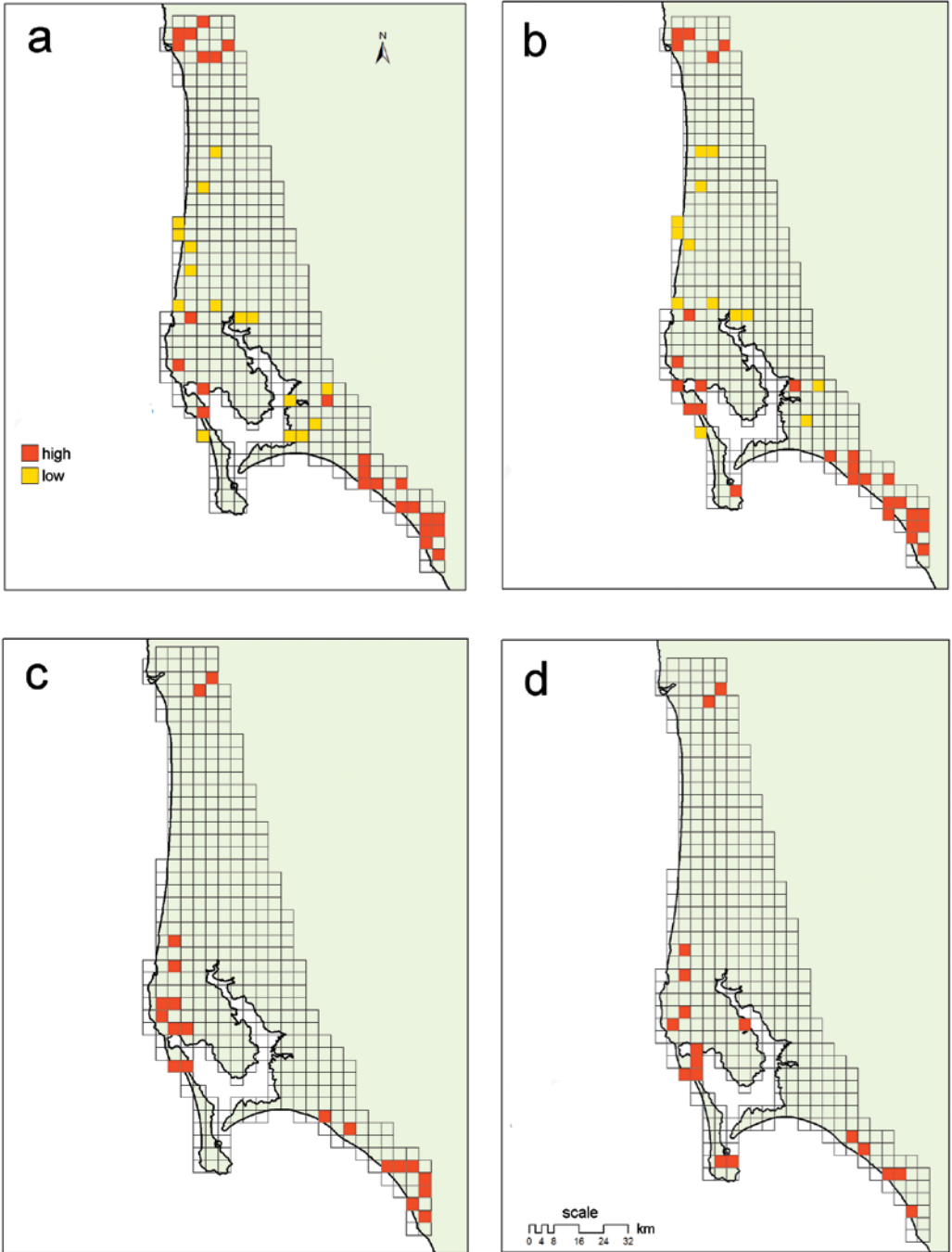


Fig. 3. Spatial pattern of 206 cells with significantly higher (red) and lower (yellow) species richness than expected using Pearson's residuals ($P < 0.01$) to test departure from random distributions for (a) all species; (b) native species; (c) endemic species; (d) rare species.