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The California Hotspots Project: identifying regions of rapid diversification of mammals

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Abstract

The high rate of anthropogenic impact on natural systems mandates protection of the evolutionary processes that generate and sustain biological diversity. Environmental drivers of diversification include spatial heterogeneity of abiotic and biotic agents of divergent selection, features that suppress gene flow, and climatic or geological processes that open new niche space. To explore how well such proxies perform as surrogates for conservation planning, we need first to map areas with rapid diversification — 'evolutionary hotspots'. Here we combine estimates of range size and divergence time to map spatial patterns of neo-endemism for mammals of California, a global biodiversity hotspot. Neo-endemism is explored at two scales: (i) endemic species, weighted by the inverse of range size and mtDNA sequence divergence from sisters; and (ii) as a surrogate for spatial patterns of phenotypic divergence, endemic subspecies, again using inverse-weighting of range size. The species-level analysis revealed foci of narrowly endemic, young taxa in the central Sierra Nevada, northern and central coast, and Tehachapi and Peninsular Ranges. The subspecies endemism-richness analysis supported the last four areas as hotspots for diversification, but also highlighted additional coastal areas (Monterey to north of San Francisco Bay) and the Inyo Valley to the east. We suggest these hotspots reflect the major processes shaping mammal neo-endemism: steep environmental gradients, biotic admixture areas, and areas with recent geological/climate change. Anthropogenic changes to both environment and land use will have direct impacts on regions of rapid divergence. However, despite widespread changes to land cover in California, the majority of the hotspots identified here occur in areas with relatively intact ecological landscapes. The geographical scope of conserving evolutionary process is beyond the scale of any single agency or nongovernmental organization. Choosing which land to closely protect and/or purchase will always require close coordination between agencies.

Keywords: California, conservation, evolutionary hotspot, Mammalia, origination, speciation

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Introduction

The assessment of biodiversity pattern in order to prioritize areas for conservation has become an increasingly sophisticated science (Margules & Pressey 2000; Sarkar *et al*. 2006). However, given the rate of anthropogenic change in environments at all scales, it is clear that to sustain biological diversity we also need to protect the ecological and evolutionary *processes* that sustain and generate diversity (Frankel 1974; Smith *et al*. 1996; Cowling & Pressey 2001; Moritz 2002). This is a substantial challenge, as we ultimately need to identify the key processes for the system in question, and then the landscape and environmental surrogates with which to represent them spatially. In relation to evolutionary processes, emphasis has been placed on identifying regions that maintain rapid adaptive evolution, concentrations of historically isolated populations (i.e. phylogeographical lineages), or both. Mapping spatial patterns of phylogenetic diversity (PD; Faith 1992) has been the subject of much recent effort, the assumption being that areas that capture the maximum

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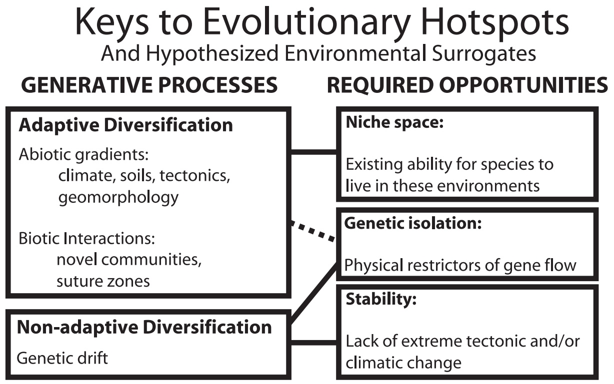

Fig. 1 Hypothesized relationship between physical environment and evolutionary landscape.

branch length for a given taxonomic group will also have the greatest trait diversity, and thus potential to respond evolutionarily to future environmental change (e.g. Forest *et al*. 2007). As a complement to the PD approach, we suggest that emphasis should be placed on protecting landscape features that promote rapid diversification, i.e. diversity potential (DP). Others (e.g. Erwin 1991) have argued for the protection of rapidly speciating clades; the difference here is the emphasis on environmental features rather than on specific taxonomic lineages. The best developed case to date concerns the diverse and rapidly evolving flora of the Cape Floristic Region of South Africa. For this biome, major environmental surrogates included edaphic, topographic, and macroclimate gradients, and emphasis was placed on identifying habitat corridors that will maintain capacity for migration and gene flow across such gradients (Cowling & Pressey 2001; Rouget *et al*. 2003, 2006). In another context, ecologically stable montane areas were identified as foci of recent speciation in African birds (Fjeldsa & Lovett 1997).

More generally, we can look to the large body of empirical and theoretical studies in evolutionary biology to identify the processes that promote rapid diversification (Fig. 1). Put simply, the key generative process is spatially heterogeneous, divergent selection. This can arise from heterogeneity in the abiotic environment (e.g. soils, climate), biotic interactions (e.g. sexual selection, Price 1998; co-evolutionary hotspots, Thompson 1999; suture zones, Remington 1968; Stebbins 1972; Rieseberg *et al*. 1999), or both. Nonadaptive divergence, through genetic drift in isolates, can also contribute to diversification, but is typically a more gradual process (Gavrilets 2003). Whether these generative processes translate into speciation depends on a number of factors. Genetic isolation, achieved through some form of assortative mating (Kirkpatrick & Ravigne 2002), most often geographical separation, facilitates adaptive modes of speciation and is essential for non-adaptive (i.e. drift) mechanisms. Nascent species also depend on available niche space if they are to persist, and this is most prevalent in novel environments as generated through geological or climatic change. Conversely, as nonadaptive diversification is typically a slow process, we expect to see concentrations of historically isolated populations in areas of environmental stability — especially Quaternary refugia (Moritz 2002). This schematic model (Fig. 1) provides a framework for interpreting observed patterns of endemism and for identifying environmental surrogates for evolutionary processes. Of course, the current geographical distributions of taxa are likely to differ from their distributions at the time of origination, but by focusing on young taxa with inferred recent divergence, we can begin to isolate the environmental conditions conducive to diversification. Observing coincident distributions of young taxa across several independently evolving lineages would add weight to this argument.

Our central aim here is to identify ‘evolutionary hotspots’ — geographical areas representing rapid diversification — within California, itself recognized as a globally significant hotspot of biological diversity (Myers *et al*. 2000). In this way, we can begin to prioritize areas of higher DP for conservation. California is well known for its high richness and endemism of species (e.g. 30% of 4839 plant species are endemic, as are 8% of the 804 vertebrate species; Stein *et al*. 2000). This, no doubt, reflects the extraordinary environmental heterogeneity of the region, combined with its dynamic geological and climatic history (Raven & Axelrod 1974; Jacobs *et al*. 2004). Previous studies on geographical patterns of endemism have focused on plants and identified divergent concentrations of palaeo- vs. neo-endemism (Stebbins & Major 1965; Raven & Axelrod 1978). Palaeoendemic plants, identified as taxonomically remote lineages, tended to be concentrated in areas with moderate to high summer rainfall (i.e. the Siskiyou–Trinity Mountains of northern California, and the northern and eastern margin of the Colorado Desert in the south). Conversely, neoendemic species — inferred as polyploid derivatives — were concentrated in areas with low summer rainfall and ecotones, e.g. the inner Coast Ranges. Thus, it was proposed that recent diversification of plants in California has been driven by the relatively recent (Plio–Pleistocene) development of a Mediterranean-type climate in the region. By contrast, for the fauna of California, scant attention has been given to patterns of species endemism *within* the state, although there have been prominent analyses of individual taxa (e.g. gophers, Patton & Smith 1990; salamanders, Wake 2006). However, state-wide analyses of comparative phylogeography have revealed congruent patterns in the distribution of historically isolated populations (Calsbeek *et al*. 2003; Lapointe & Rissler 2005), and highlighted areas of the state with high concentrations of narrowly endemic phylogeographical lineages (Rissler *et al*. 2006).

Here, we focus on spatial patterns of endemism in the mammals of California. The state has a rich mammal fauna and also has the largest number of fully endemic species of any state within the USA (185 species, of which 18 are fully endemic; Stein *et al*. 2000). The fauna includes some taxa, such as pocket gophers (*Thomomys*, Patton & Smith 1990) that exhibit spectacular levels of geographical diversity and others with multiple narrowly distributed species (e.g. *Dipodomys* kangaroo rats, *Tamias* chipmunks).

In particular, and following Stebbins & Major (1965), our aim is to identify geographical areas with concentrations of neo-endemic taxa. We do this at two taxonomic scales. First, for species that are endemic or near-endemic (> 75% of range in California), we use molecular (mtDNA) phylogenies with dense sampling of congeners to estimate relative divergence times. Combined with fine-scale (1 km^2) estimates of distributions, we then map inverse range- and divergence-weighted endemism to locate geographical hotspots of recently diverged taxa. Second, for endemic or near-endemic subspecies, we use distributional information alone to estimate geographical patterns of inverse range-weighted richness. Subspecies, identified as morphologically differentiated yet intergrading sets of populations, have long attracted the attention of students of speciation because they often represent a stage of phenotypic diversification preceding full speciation (Grinnell 1928; Lidicker 1960; Mayr 1982; Patton & Smith 1990). Some have argued that such morphologically defined subspecies have limited utility for diversity analyses because they often do not correspond with historical subdivisions within species (Zink 2004; but see Phillimore & Owens 2006). However, in the context of our present study, which seeks to identify geographical foci of rapid diversification, it is exactly this emphasis on spatially bounded phenotypic differentiation that we wish to capture as a surrogate for adaptive divergence. Indeed, cases where strong morphological discontinuities are evident but genetic divergence is minimal are of particular interest as they attest to recent phenotypic evolution or to divergence in the face of ongoing gene flow.

Materials and methods

Molecular data for species-level analysis

Twenty-five species have > 75% of their geographical range in California (Hall 1981), and for all of these but one (*Ammospermopholis nelsoni*), there are published or unpublished mtDNA phylogenetic hypotheses with taxon sampling sufficient to allow estimation of sequence divergence from their respective sister group (Table 1). We obtained relevant sequence data — mostly cytochrome *b*, but also cytochrome subunits 1 or 3 in some cases — from GenBank and/or unpublished studies. Using MEGA version 3.1 (Kumar *et al*. 2004), sequences were aligned within each genus (using the CLUSTAL W plugin with default parameters and subsequent visual inspection). For taxa with multiple individuals sequenced, we estimated net Tamura–Nei (1993) (TN) distances to the sister taxon; otherwise, simple pairwise distance was calculated. Although there is likely to be some variation among lineages in mtDNA substitution rates, this will have little effect at low divergence levels (which receive the highest weight) and we have not attempted to correct for this here. For species sister to a larger clade, we recorded the average of the distances from the endemic to the members of its sister clade. Because one cannot generally identify which is the derived species, we included both sister taxa if they meet our criterion for endemism. The inverse of these TN distances were used as weights for the construction of maps of neoendemism; that is, all gridcells for a species' range were multiplied by 1/TN for that species. In this way, the ratios of genetic distances between species were preserved, but weights were applied so that shorter distances between sisters produced higher values.

Distribution data for species- and subspecies-level analyses

For each of the focal species (N = 25; Table 1) and subspecies (N = 133; Appendix I), we extracted point distribution data from the Museum of Vertebrate Zoology (MVZ) database. Much of the georeferencing of MVZ mammal data took place as a result of the Mammal Networked Information System (MaNIS) project (http://manisnet.org). We did not include the one species (*Urocyon littoralis*) and 13 subspecies endemic to one or more of the Channel Islands because their necessarily small ranges would have disrupted the range-weighted analyses of endemism across the continental area. This should not be taken to suggest that island taxa are not important for either the endemism of an area or for conservation of evolutionary processes.

Our analysis rests upon voucher-backed museum records. For both species and subspecies, occurrence data from the MVZ database (http://mvzarctos.berkeley.edu/) were downloaded after mapping (using BERKELEYMAPPER http://berkeleymapper.berkeley.edu/) to restrict records to those for which latitude and longitude coordinates were available. Prior to analysis, we used multiple approaches to detect and remove unreliable records. Geographical outliers, detected using BERKELEYMAPPER, were checked and either corrected (if obviously entry errors) or omitted. Records with maximum uncertainty estimates greater than 13.6 km (the 90th percentile for all localities) were removed from our data set. As a final test for our occurrence data, taxon records were checked for environmental outliers using DIVA-GIS (http://www.DIVA-GIS.org/; annual temperature, annual precipitation, extreme quarters for temperature and

Table 1 List of included mammal species, their Tamura–Nei distances to sisters, relevant publications, and model statistics

Scientific name	Tamura–Nei	Gene(s) used	Reference	Sister taxon/taxa	AUC	Kappa	Area	*n* for modelling
Sorex lyelli	0.017*	Cyt *b*	J.L.P. unpublished data	*S. preblei*	1.00	1.00	4498	30
Sorex ornatus	0.077	Cyt *b*	Demboski & Cook (2001)	*S. vagrans*	0.81	0.52	25521	52
Thomomys monticola	0.083	Cyt *b*	J.L.P. unpublished data; Spradling *et al*. (2004)	*T. talpoides, T. mazama*	0.96	0.86	72960	263
Chaetodipus californicus	0.098	Cyt *b*	J.L.P. unpublished data; Alexander & Riddle (2005)	*C. arenarius*	0.79	0.48	150309	161
Dipodomys agilis	0.012	Cyt *b*	J.L.P. unpublished data; Alexander & Riddle (2005)	*D. simulans*	0.95	0.78	74610	106
Dipodomys californicus	0.138	Cyt *b*	J.L.P. unpublished data; Alexander & Riddle (2005)	*D. agilis, D. gravipes, D. heermanni, D. ingens, D. microps, D. panamintus, D. simulans, D. stephensi, D.venustus*	0.94	0.79	74610	176
Dipodomys heermanni	0.034	Cyt *b*	J.L.P. unpublished data; Alexander & Riddle (2005)	*D. panamintus*	0.90	0.70	91403	12
Dipodomys ingens	0.145†	Cyt *b*	Alexander & Riddle (2005)	*D. microps*	0.95	0.89	9379	59
Dipodomys nitratoides	0.070	Cyt *b*	J.L.P. unpublished data; Alexander & Riddle (2005)	*D. insularis, D. margaritae, D. merriami*	0.98	0.91	18516	87
Dipodomys panamintus	0.034	Cyt *b*	J.L.P. unpublished data; Alexander & Riddle (2005)	*D. heermanni*	0.98	0.95	77665	10
Dipodomys stephensi	0.085‡	Cyt *b*	J.L.P. unpublished data; Alexander & Riddle (2005)	*D. panamintus, D. heermanni*	0.92	0.81	4498.3	46
Dipodomys venustus	0.097	Cyt *b*	J.L.P. unpublished data; Alexander & Riddle (2005)	*D. agilis, D.simulans*	0.93	0.86	23786	318
Perognathus alticola	0.026[b]	Cyt *b* and CO3	Alexander & Riddle (2005)	*P. pavus* -Utah	0.97	0.96	2154	155
Perognathus inornatus	0.050	Cyt *b*	J.L.P. unpublished data	*P. longimemberis*	0.90	0.77	194450	7
Arborimus pomo	0.030	Cyt *b*	Bellinger *et al*. (2005)	*A. albipes*	0.98	0.93	29215	270
Microtus californicus	0.123[b]	Cyt *b*	Conroy & Cook (2000)	*M. mexicanus*	0.75	0.37	392395	75
Neotoma fuscipes	0.063	Cyt *b*	Matocq *et al*. (2007)	*N. macrotis*	0.80	0.54	230434	47
Peromyscus californicus	0.140§	CO3	Riddle *et al*. (2000)	*P. eremicus, P. eva, P. merriami*	0.84	0.56	97096	10
Reithrodontomys raviventris	0.149[b]	Cyt *b*	Arellano *et al*. (2005)	*R. montanus*	0.98	0.96	4325	138
Ammospermophilus nelsoni	N/A				0.97	0.86	12692	7
Spermophilus mojavensis	0.042[a]	Cyt *b*	Harrison *et al*. (2003)	*S. tereticaudus*	0.99	0.95	25521	56
Tamias alpinus	0.014	Cyt *b*	Rubidge personal communication; Piaggio & Spicer (2001)	*T. minimus*	0.99	0.97	9256	152
Tamias merriami	0.044	Cyt *b*	Rubidge personal communication; Piaggio & Spicer (2001)	*T. obscurus*	0.86	0.60	82497	55

Table 1 *Continued*

Scientific name	Tamura–Nei	Gene(s) used	Reference	Sister taxon/taxa	AUC	Kappa	Area	*n* for modelling
Tamias ochrogenys	0.035	Cyt *b*	Rubidge personal communication; Piaggio & Spicer (2001)	*T. townsendii*	0.98	0.94	11193	46
Tamias quadrimaculatus	0.056	Cyt *b*	Rubidge personal communication; Piaggio & Spicer (2001)	*T. speciosus*	0.97	0.94	35419	22
Tamias senex	0.033¶	Cyt *b*	Rubidge personal communication; Piaggio & Spicer (2001)	*T. ochrogenys*, *T. sonomae*, *T. townsendi*	1.00	0.98	89644	119
Tamias sonomae	0.025	Cyt *b*	Rubidge personal communication; Piaggio & Spicer (2001)	*T. senex*	0.97	0.87	52384	219
Tamias speciosus	0.049	Cyt *b*	Rubidge personal communication; Piaggio & Spicer (2001)	*T. aplinus*, *T. minimus*, *T. panamintinus*	0.95	0.84	50387	178

*Two individuals for each species.

†Pairwise distances between individuals.

‡One individual of *D. stephensi*, but net distance to other spp.

§One individual of *P. merriami*, but net distance to other spp.

¶Paraphyly of *T. senex* suggests it is actually a palaeoendemic ancestor of *T. townsendi*, *T. ochrogenys*, and *T. sonomae*.

precipitation) and cut at the 25th percentile. For the remaining data, all duplicate localities were deleted. Taxa with fewer than five records were not included in our species level analysis and were not modelled for subspecies (see section on niche modelling for their treatment).

Environmental data, niche modelling and range inference

To generate the fine-scale (1 km^2) estimates of species distribution necessary for subsequent analyses, we used a hybrid approach, combining species distribution models generated from presence records with estimates of range boundaries inferred from expert range maps and/or buffered points (Graham & Hijmans 2006). Given its strong performance in tests using presence-only records (Elith *et al*. 2006), we used maximum entropy distribution modelling (MaxEnt; Phillips *et al*. 2006) to estimate geographical ranges from the occurrence data. Twenty environmental variables were used in the initial modelling, all at 1 km resolution and clipped to a bounding box for our analysis (53.70001N and 19.23334S latitudes; –137.87076W and –94.92090E longitudes). Standard bioclimatic variables for temperature and precipitation were used, derived from the global data set Worldclim (Hijmans *et al*. 2005) with the addition of altitude (SRTM 30 arc second, *c*. 1 km resolution).

To model species distributions for each species and subspecies, we used MaxEnt 2.3 (Phillips *et al*. 2006) with the following options: jackknife, 25% testing, remove duplicates. Receiver operating characteristic (ROC) curves, area under curve (AUC) and Kappa values were calculated to evaluate model performance. To minimize overprediction, we cut predicted species ranges using a combination of established range maps from NatureServe (Patterson *et al*. 2005) and 10 km buffers around the MVZ point data. We kept all probability information from MaxEnt, to provide additional precision to our maps of endemism. For the subspecies data, we cut the predictions using a combination of 100 km buffers around minimum convex polygons built on the original point data and a probability threshold for each taxon that maximized Kappa; the latter preventing range estimates from overpredicting within the 100-km buffer. Eight of the 133 subspecies with $n < 7$ geographically unique records had environmental outliers included to increase sample size (Appendix I). Seven subspecies had ranges too small to provide the geographical sampling required for this method of range estimation. For these taxa (Appendix I), we estimated presence–absence distributions based on both the confirmed location of MVZ specimens and the field experience of J.L.P.

Compilation of endemism maps

We were able to construct four types of endemism maps from species ranges and two from subspecies ranges. All included the MaxEnt probability surface to put more weight on cells with high levels of predicted occurrence. The first is simple richness, i.e. the number of species or subspecies in each 1 km grid cell. The second is richness weighted by the inverse of range size in km^2, normalized by the taxon with the smallest area (cf. Williams *et al*. 1993). Normalizing by the smallest area restricts the weight values to the range [0–1] and removes the effect of units on the values of map cells. These 'richness endemism' maps emphasize areas with concentrations of geographically restricted endemic taxa and have a direct relationship to complementary — a key driver in systematic conservation planning (Kier & Barthlott 2001). For species only, we then produced two additional types of endemism maps, richness weighted by the inverse of sequence divergence (neo-endemism) and richness weighted by both the inverse of sequence divergence and the inverse of taxon area (neo-endemism richness). The inverse sequence divergence values are normalized to the shortest distance, again confining the values to the range [0–1].

Results

Estimation of geographical ranges

In general, we were able to obtain robust estimates of distribution from the filtered point occurrence data (Table 1). For the species models, AUC averages 0.93 ± 0.07 (± SD) and kappa values average 0.81 ± 0.18. *Microtus californicus* has the lowest AUC (0.75) and kappa (0.37). *Sorex lyelli* has the highest AUC (1.00) and kappa (1.00). For MaxEnt models of subspecies, the AUC averages 0.95 ± 0.055 and kappa values average 0.86 ± 0.131. Several subspecies have AUC and kappa values at or near 1, as a consequence of the small number of training and testing points available. These subspecies have known attenuated ranges, so we have included them in our analysis despite their artificially high statistics. *Lepus californicus bennettii* has the lowest AUC (0.69) and kappa (0.32) of the subspecies. Of course, the seven restricted-range subspecies based on expert-opinion maps have no AUC or kappa values.

The estimated geographical areas for California endemic species (Table 1) are log-normally distributed, with a mean of 78 928 km^2 and a standard deviation of 91 615 km^2. The species with the largest distribution is *M californicus* (392 394 km^2) and the species with the smallest distribution is *Perognathus alticolus* (2154 km^2). The geographical areas for subspecies (Appendix I) are log-normally distributed, with a mean of 34 274 km^2 and a standard deviation of 36 342. The subspecies with the largest distribution is *Canis latrans ochropus* (172 493 km^2) and the MaxEnt-modelled subspecies with the smallest distribution is *Microtus californicus halophilus* (317 km^2). The seven subspecies with so few records that we used expert maps rather than modelling had estimated ranges of between 6 km^2 (*Perognathus alticolus alticolus*) and 856 km^2 (*Sorex ornatus relictus*) (Appendix I).

Sequence divergence of endemic species

We were able to estimate mtDNA sequence divergence for 27 of the 28 mammal species endemic or near-endemic to California, the exception being *Ammospermophilus nelsoni*. Using net sequence divergence for 23 taxa and simple pairwise divergence for the four taxa for which only single individuals have been sequenced (Table 1), divergence values between the endemic species and their sister taxa are log-normally distributed, with a mean of 0.066 and a standard deviation of 0.043. *Dipodomys agilis* has the shortest TN distance, 0.012, and *Reithrodontomys raviventris* has the longest distance, 0.149. The two most speciose genera in our analysis, *Dipodomys* and *Tamias*, show contrasting evolutionary histories of diversification; *Dipodomys* has consistently longer branch lengths (mean = 0.08), whereas the Californian endemic species of *Tamias* have much lower sequence divergence to their sister groups (mean = 0.04), and thus contribute much more strongly to patterns of neo-endemism (see below). There is no relationship between TN distance and geographical area ($r = 0.20$, $P = 0.30$) or log area ($r = 0.08$, $P = 0.69$).

Mapping of species level diversity

Species richness. Geographical richness for the 28 species of mammals regarded as endemic or near-endemic to California (Fig. 2A) is highest across the central and southern Coast Ranges and adjacent montane regions — the Tehachapi, Transverse and Peninsular Ranges. To a large extent, this pattern of higher richness to the west of the study area is to be expected given the selection of endemic and near-endemic species. Five widely ranging endemic species occur across most of this high richness area (*M. californicus*, *S. ornatus*, *Tamias merriami*, *Chaetodipus californicus*, *Peromyscus californicus*). Individual subsets of this area of high richness are each supported by at least one taxon restricted to that area (Appendix II). *R. raviventris* contributes only to the San Francisco (SF) Bay Area subregion; *A. nelsoni*, *Dipodomys ingens*, and *Dipodomys nitratoides* only to the intersection of the San Joaquin Valley (southern Central Valley in Fig. 2A) and the southern Coast Range; *P. alticolus* only to the Tehachapi and Transverse Ranges; and *Dipodomys stephensi* only to the Peninsular Range.

Endemism richness. Weighting of the selected species by the inverse of range size (Table 1) highlights six hotspots with concentrations of narrowly distributed taxa: the SF Bay Area, the southwestern San Joaquin Valley, a narrow montane band connecting the Tehachapi and Inner Coast Ranges, the Peninsular Ranges, the central Sierra Nevada, and the North Coast (Fig. 2B, Appendix II). For each of these areas, there are particular species that dominate the endemism-richness analysis. The SF Bay Area is highlighted because of *R. raviventris*, which is restricted to the salt marshes around the bay. For the southwestern San Joaquin Valley, *D. ingens* dominates the signal, but *A. nelsoni* and *D. nitratoides* reinforce it. The Tehachapi and San Bernardino Ranges are highlighted by *P. alticolus* alone, the species with the smallest geographical range in our analysis. The Peninsular Range hotspot, centred on the San Jacinto Valley, is driven by *D. stephensi*. The central Sierra Nevada hotspot, which was not evident from patterns of species richness alone (cf. Fig. 2A, B), is driven by two restricted range species — *S. lyelli* and *Tamias alpinus*. The northern Coast Ranges, unlike the other hotspots, depend on the co-occurrence of several medium-ranged species rather than one or two very restricted species, these being *Tamias ochrogenys*, *Arborimus pomo* and *Tamias sonomae* and, to a lesser extent, *Dipodomys californicus*.

Neo-endemism. Weighting of species occurrences by the inverse of sequence divergence (Fig. 2C) accentuated the Central Coast, Tehachapi, Transverse, and Peninsular Ranges, along with the central and southern Sierra Nevada. This reflects the presence of relatively recently evolved species in each area; these are *D. agilis*, *D. panamintus*, *P. alticolus*, *T. merriami*, and *Tamias speciosus* for the Tehachapi, Transverse, and Peninsular Ranges; and *S. lyelli* and *T. alpinus* for the central Sierra Nevada (Table 1, Appendix II). When species are weighted by the inverse of both sequence divergence and geographical range (i.e. neo-endemism richness), five hotspots are apparent: the Tehachapis, the San Bernardino Mountains in the Transverse Ranges, San Jacinto Valley within the Peninsular Ranges, the central Sierra Nevada, and the northern Coast Ranges (Fig. 2D). As for the endemism-richness analyses, the Tehachapi, San Bernadino, San Jacinto Valley, and central Sierra Nevada hotspots are driven by a small number of species. The Tehachapi hotspot is driven by *P. alticolus*, but *D. agilis, T. merriami,* and *T. speciosus*, all species ranging into the Tehachapis from other regions, add support. The hotspot in the San Bernardino Mountains reflects the southernmost disjunct population of *P. alticolus*, which may be already extirpated (Williams 1986). The San Jacinto Valley hotspot reflects the distribution of *D. stephensi*. The central Sierra Nevada hotspot is dominated by *S. lyelli* and *T. alpinus*, both species with restricted ranges and short branch lengths, and is reinforced by the wide-ranging, but recently evolved *T. speciosus.* The contrast between the central Coast Ranges and the adjacent western San Joaquin Valley is instructive. The latter was strongly represented in the endemism-richness analysis because of the presence of

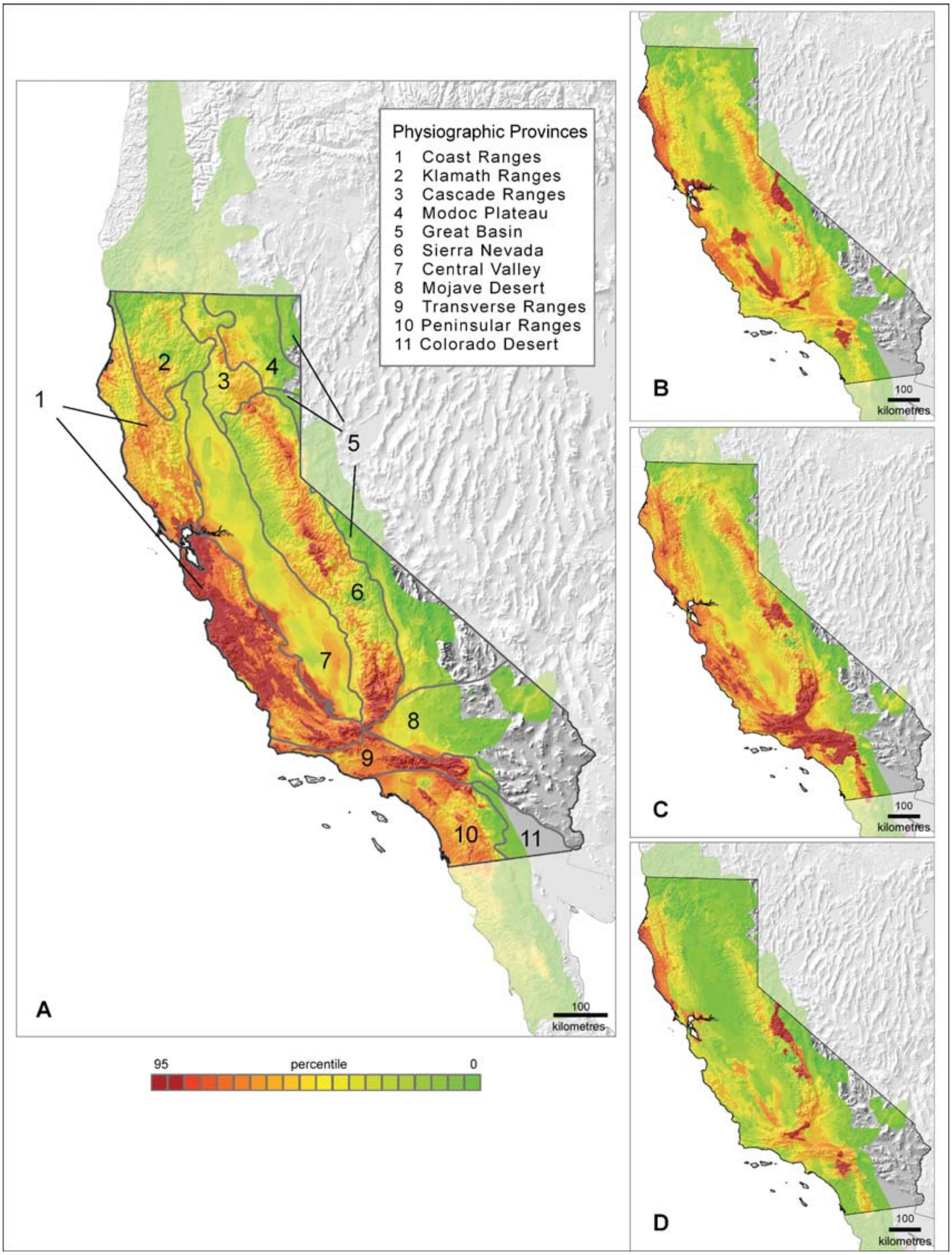

Fig. 2 Species-level maps of mammalian endemism. (A) Unweighted richness with physiographic provinces. (B) Endemism-richness (weighted by area^{-1}). (C) Neo-endemism (weighted by TN depth^{-1}). (D) Neo-endemism richness (weighted by area^{-1} and TN depth^{-1}).

narrowly distributed species of *Dipodomys* (*D. ingens* and *D. nitratoides*), but these show large to moderate sequence divergence from their sister taxa (genetic data are lacking for the third species relevant to this area — *A. nelsoni*). By contrast, the central Coast Ranges have higher values than the San Joaquin Valley in the neo-endemism analysis, supported by the overlap of several wide-ranging, recently diverged species: *Dipodomys heermani*, *Perognathus inornatus* and *T. merriami*. These two contrasting patterns cancel out in the neo-endemism richness analysis, leaving

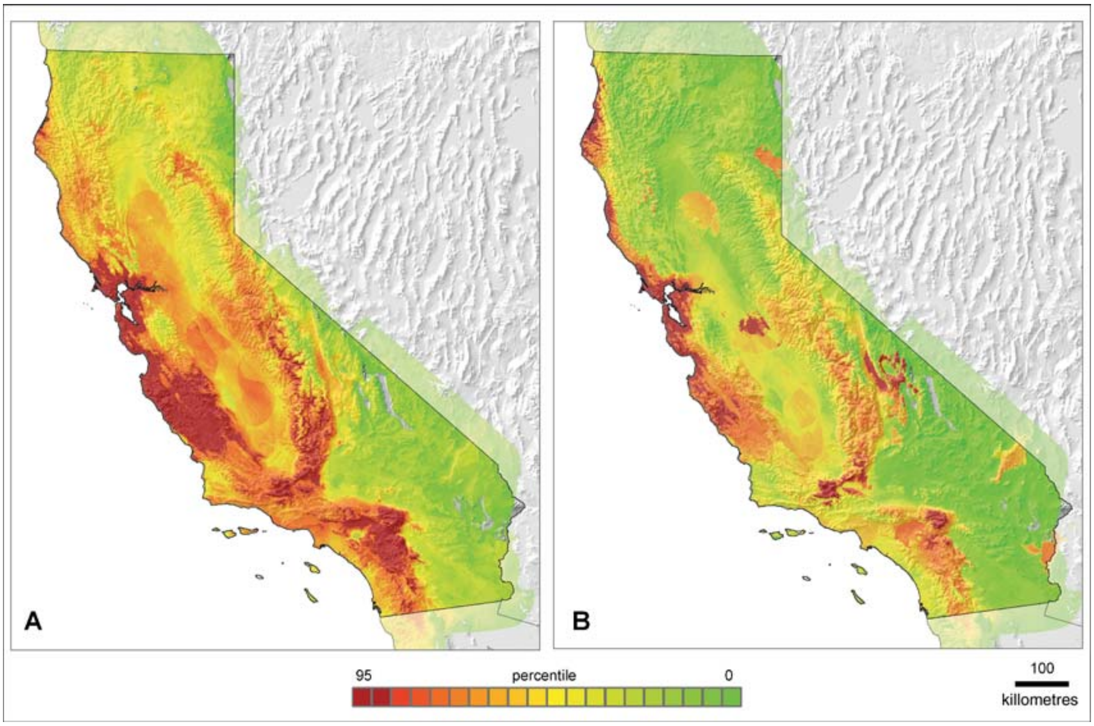

Fig. 3 Subspecies-level maps of mammalian endemism. (A) Unweighted richness. (B) Endemism richness (weighted by area^{-1}).

no hotspots in the central coast and San Joaquin Valley. The neo-endemism richness hotspot of the northern coast is dominated by *T. ochrogenys* and *A. pomo*. As with the endemism-richness analysis, this hotspot is created by several medium-value taxa co-occurring and not a single, small-ranged short-branched species. *R. raviventris*, important to making the SF Bay Area a hotspot in the richness and endemism-richness analyses, is deemphasized in the neo-endemism and neo-endemism richness analyses because of its relatively long branch length.

Mapping of subspecies endemism

As for species, the maximum richness of subspecies endemic to California is along the central coast from the San Francisco Bay Area, south through the Santa Lucias and inner Coast Ranges, the Tehachapi, Transverse, and Peninsular Ranges, and the central to southern Sierra Nevada (Fig. 3A). When subspecies are weighted the inverse of geographical range size (i.e. subspecies endemism-richness; Fig. 3B), several hotspots of phenotypic differentiation emerge. There are multiple hotspots along the Coast Ranges; two in the northern Coast Range, one in the SF Bay Area, and one in the central Coast. As for the species-level analyses, hotspots are evident in the Tehachapi and San Bernardino Ranges. Unique to the subspecies analysis are additional foci of differentiation in the Owens Valley area (east of the southern Sierra Nevada), and in the Central Valley on the San Joaquin River. These hotspots break down into those dominated by a single, small-ranging taxon, those driven by multiple small-ranging taxa, and those supported by a large number of medium-ranged taxa (Appendix I). The two hotspots dominated by a single subspecies are those in the Central Valley and the more southerly region of the northern Coast Range. The remaining hotspots, save one, are driven by several smaller-ranging taxa, ranging between 13% and 36% of the subspecies present (Appendix I). The last hotspot is the one in the central Coast Ranges area, running along the Santa Lucia Range; this hotspot is supported by 14 of the 28 subspecies present, a very different pattern from all of the others.

Discussion

Limitations of analysis

Our primary goal here was to identify geographical regions that represent foci of recent divergent evolution of mammals in California, and so inform future identification of environmental surrogates for evolutionary hotspots (e.g. Fig. 1) and planning for conservation initiatives. Before discussing the results themselves, we highlight some limitations inherent to such analyses. One potential limitation is with the quality of range information for individual taxa. All records used were backed by voucher specimens (in the MVZ), so that we can have confidence in their taxonomic identification, and georeferencing has been done to modern standards (Wieczorek *et al*. 2004). Nonetheless, some potential errors were detected by outlier analysis and these records were omitted. Following Graham & Hijmans (2006), we used a hybrid approach that intersects modelled ranges with range maps to provide the best possible, high-resolution estimates of distribution.

The use of mtDNA sequence divergence as a surrogate for relative divergence time is a second limitation of this study. Even allowing for the assumption of uniform rates of sequence divergence, any such single gene estimates of divergence time are prone to error because of unquantified differences between times of gene-coalescence and lineage-divergence (Edwards & Beerli 2000). Typically, we estimated net sequence divergence which should, to some extent, correct for the differences between the two (Wilson *et al*. 1985), but we acknowledge that in many cases we may be overestimating true divergence time. On the other hand, if there has been introgression of mtDNA among species, as proposed for some of these genera (e.g. Rocky Mountain *Tamias*, Good *et al*. 2003), then lineage divergence time will be underestimated. Collectively, we expect that the combined sources of error will add noise, rather than bias. More precise estimates of divergence time could, of course, be obtained using multilocus estimates and coalescent methods (e.g. Hey & Nielsen 2004), but those are beyond the scope of the present analysis.

The final area of potential concern is whether subspecies have been delineated using consistent criteria. While this might be a problem in general, much of the present taxonomy for Californian mammals has common roots in the work of Grinnell and his intellectual descendents, and so is reasonably consistent in approach. For example, of the taxa with the largest numbers of described subspecies, the current subspecies of chipmunks ($N = 12$ Californian taxa) were reviewed systematically by Johnson (1943), *Dipodomys* ($N = 20$) by Grinnell (1922) and Lidicker (1960) and *Chaetodipus* ($N = 10$ taxa) by Benson (1933). By far, the most problematic group, gophers of the *Thomomys bottae* group, were examined in detail by Patton & Smith (1990) using a philosophy similar to that of Grinnell, but with much richer data and improved analytical methods, resulting in a reduction of the number of recognized subspecies within California from 46 to 15.

Identification and implications of hotspots

Although there is some disagreement in the details, all of the analyses (Figs 2–4) indicate that California contains several hotspots of endemism. The concentration of richness of Californian endemic or near-endemic species along coastal areas and associated mountain ranges likely reflects the geographical criteria for taxon-selection, and we do not ascribe any special significance to it. Within this area, five hotspots are supported by both the neo-endemism analysis of species and endemism-richness of subspecies: the Tehachapi Ranges, the San Bernardino Range, at Bodega Bay on the north coast, parts of the Santa Cruz Mountains and the Santa Lucia Range of the central coast, northeastern Transverse and Tehachapi Ranges east to the Piute Mountains, and the San Bernardino Range into the San Jacinto Valley (Fig. 4). Beyond these, the analyses of species and subspecies reveal geographically distinct foci of recent diversification. The former exhibit a unique concentration of neo-endemism in the central Sierra Nevada, whereas the latter show hotpots of endemism in the north coast, San Francisco Bay Area and the Owens Valley to the east (Fig. 4).

The observed hotspots are generated by two patterns. The first of these patterns is a hotspot created by high species richness in an area where many taxa of medium range size or divergence intersect. In particular, the patterns across most of the California coast, except for the SF Bay Area, fit this profile, since the coastal and Coast Range hotspots are never dominated by a single species or subspecies.

The area of the Central Coast and southern Coast Ranges are of particular interest to scholars of California endemism, since they were highlighted by the seminal work of Stebbins & Major (1965) as containing hotspots of neo-endemism in vascular plants. On the whole, our results agree with theirs, but ours suggest more of a concentration of neo-endemic species and a concentration of narrow-range subspecies on the western, coastal side of the region. By contrast, plant neo-endemism was concentrated in the inner Coast Range, approaching the Central Valley, leading Stebbins & Major (1965) to suggest that the change to the summer-dry Mediterranean climate through the Pleistocene had triggered this evolution. The mammal species of the inner Coast Range to Central Valley area tend to have longer branch lengths and smaller ranges than those on the western side, which creates a reversal from the endemism-richness to the neo-endemism maps. These species on the eastern edge of the region, several *Dipodomys* and *Ammospermophilus nelsoni*, are adapted for the arid conditions Stebbins & Major (1965) suggest are the driver of plant neo-endemism, and the substantial molecular divergence of the *Dipodomys* species suggest relatively old (perhaps Pliocene) diversification, which would link them to the Late Miocene change to summer-dry conditions. The concentration of recent speciation and phenotypic diversification in the southern Coast Range occurs in a region that, while tectonically active, may have been more environmentally stable than the interior, which contained expanded wetlands and riparian corridors in the Central Valley and permanent glaciers in the Sierra Nevada as recently as 10 000 years ago (Jacobs *et al*. 2004). This correlation of neo-endemism and stability fits with the observations of

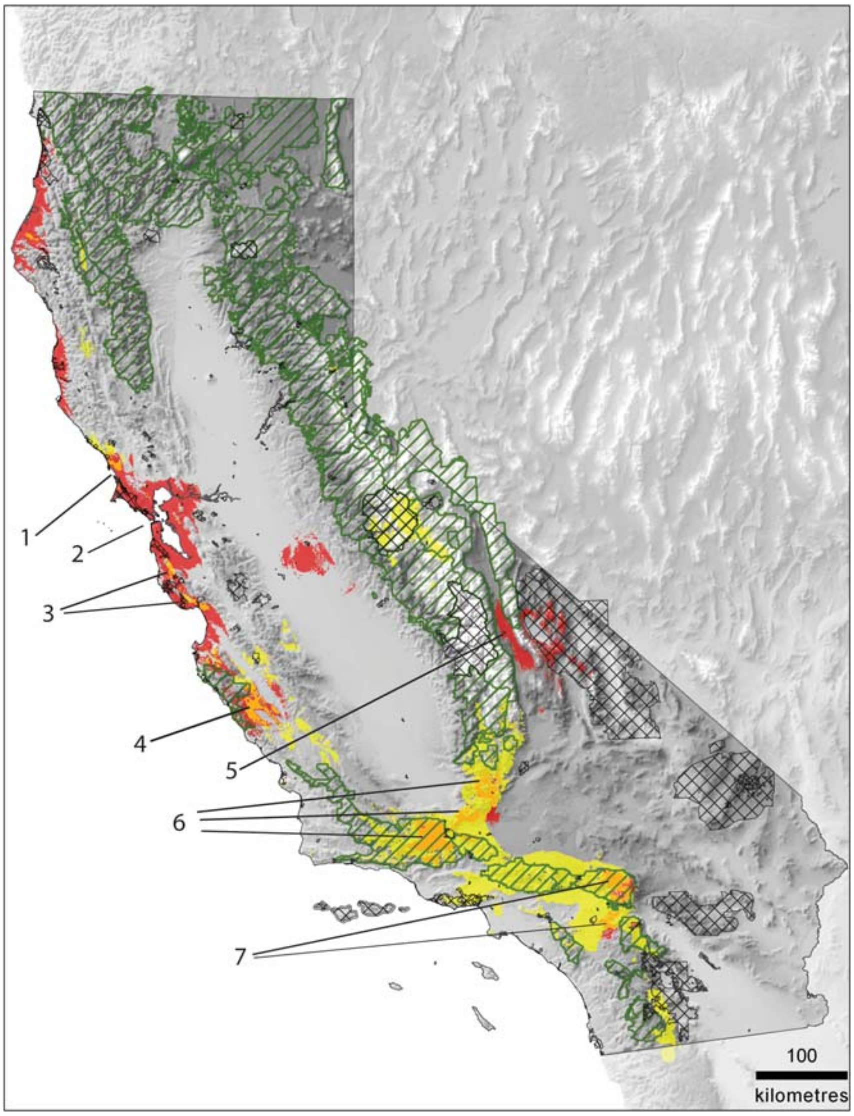

Fig. 4 Mammalian evolutionary hotspots shown in relationship with protected areas. Red areas are above the 90th percentile for subspecies endemism richness; yellow are above the 90th percentile for species neo-endemism richness; orange are areas of overlap between species and subspecies hotspots. Black cross-hatches indicate State and National Parks; green hatches show National Forests. Numbered geographical features are: 1, Bodega Bay; 2, San Francisco Bay; 3, Santa Cruz Mountains; 4, Santa Lucia Range; 5, Owens Valley; 6, northeastern Transverse, Tehachapi Ranges, and Piute Mountains; 7, San Bernardino Range and San Jacinto Valley.

Fjeldsa & Lovett (1997), who found a similar pattern in species of birds and plants in tropical Africa. Stability and steep environmental gradients are two of our suggested drivers of evolutionary process (Fig. 1), and the coincidence of these two factors in this area of elevated neo-endemism provides qualitative support to use them as environmental proxies for evolutionary hotspots.

The north coast and northern Coast Ranges show a high degree of neo-endemism, as measured using subspecies endemism-richness (Fig. 4). Species level neo-endemism is consistently elevated across these northern ranges from coast to Central Valley (although most often at less than the 90th percentile illustrated in Fig. 4), but the subspecies endemism-richness is much more localized on the coast, again suggesting the importance of steep environmental gradients towards the equitable coastal climate.

The other major pattern revealed by our analyses is that of a hotspot dominated by one or two small-ranged and/or short-branched taxa. The best example is the SF Bay Area, which is dominant in both the species- and subspecies-level endemism-richness analyses. The SF Bay Area has already been implicated as a contributor to evolutionary change because of its central location as an aquatic barrier to dispersal (Hooper 1940, 1944). The area is home to a large number of endemic subspecies, such as the salt marsh endemic of *Microtus californicus* described by Thaeler (1961), and one very prominent endemic species, *Reithrodontomys raviventris*, which has two subspecies around the bay, documented by Dixon (1909). In the maps of both species and subspecies endemism-richness, *R. raviventris* contributes most of the weight that makes the SF Bay Area a hotspot, but its long branch-length down-weights it in the neo-endemism analyses to the point that the SF Bay Area is no longer highlighted. The long branch of *R. raviventris* illustrates the complementarity between analyses of species-level neo-endemism and endemism-richness of subspecies; its highly divergent sister taxon, *Reithrodontomys montanus*, is only found in the Great Plains, yet *R. raviventris* does have two subspecies in the SF Bay Area, which suggests that local differentiation may be recent and/or ongoing. The subspecies endemism-richness data show that the SF Bay Area hotspot is supported by a variety of small-ranging subspecies, two of which belong to species that are not considered California endemics in our species-level analysis (Appendix I).

By contrast, the Tehachapi hotspot of the endemism-richness and neo-endemism seems at first to rely almost exclusively on the small, recently diverged *Perognathus alticolus*, but this is something of an illusion. Examination of the subspecies data indicates that this area is still important, even when the relative size of the range of *P. alticolus* is tempered by the many other small-ranged subspecies included in the analysis. In fact, the coincidence of so many endemic subspecies in the Transverse and Tehachapi Ranges and immediately adjacent Coast Range was noted long ago by Kellogg (1918) in his revision of *M. californicus*. The reason why this region continues to be highlighted is because it represents a crossroads of sorts between the other major regions of California: the Sierra Nevada, the Coast Ranges, the Central Valley, and the deserts of the southeast. Many species have ranges that extend from these areas into the Transverse Ranges, and it is the conjunction of these ranges (as can be seen even in the unweighted species richness map, Fig. 2A) that makes the area important. Evolutionary processes in the Transverse/Tehachapi Ranges are probably dominated by both the environmental gradients in this transitional area and by the complex biotic interactions among the populations there; as outlined in the Introduction (Fig. 1), interactions with other species can be as important for origination as interactions with the physical environment.

The hotspots in the central Sierra Nevada and the Owens Valley and adjacent ranges to the east are also created by a small number of dominant taxa. The central Sierra Nevada hotspot stems from a few recently diverged small mammals that are adapted to alpine habitats, most prominently *Tamias alpinus* and *Sorex lyelli*. It may be that the neo-endemism here is related to steep environmental gradients and open niche space concomitant with postglacial colonization (Fig. 1). The Owens Valley hotspot may reflect analogous evolutionary processes. The subspecies involved in this hotspot are extreme southern members of cool- and dry-climate adapted species from the Great Basin. The ongoing topographic evolution of Owens Valley (Pinter & Keller 1995) and the surrounding areas, coupled with the environmental gradient from the cooler northern Great Basin desert through this area to the much warmer Mojave Desert to the south, may have produced the concentration of small-ranged subspecies here.

The last small-range dominated hotspot, the hotspot of the Central Valley, is evident only from the subspecies data, since the species distributed in the Central Valley are all too widely ranging and too old to be regarded as neo-endemics. This hotspot may be associated with Pleistocene climate change, but it more likely reflects human-mediated habitat change, since the Central Valley was already highly impacted before the beginning of MVZ specimen collecting in the early 20th century. Note that many of these subspecies are riparian — a habitat type that has been highly impacted by land-cover change.

Implications for conservation in human-altered environments

Conservation priorities should be set with respect to diverse kinds of organisms, so our results for mammals alone (Fig. 4) should not be considered as representative of neo-endemism patterns for the California biota. We are currently pursuing a broader perspective, collaborating with others to analyse information concerning amphibians, reptiles and vascular plants endemic to California. Further, given that vertebrates and plants can be poor surrogates for invertebrates (e.g. Moritz *et al*. 2001), the analyses should be extended to the latter as information on species distributions and evolutionary processes accumulates (e.g. Caterino 2006; Gompert *et al*. 2006; Starrett & Hedin 2007; Vandergast *et al*. 2007). All of these kinds of organisms can be expected to respond to evolutionary processes with distinct geographical scales and environmental drivers. The ultimate goal is to synthesize across these groups to better understand how and where to protect evolutionary processes that can benefit the biological landscape as a whole.

Human modifications of ecological systems, whether through introduced species, land-cover change, or climate change, are likely to alter spatial patterns of natural selection and gene flow. Substantial areas of California have been impacted by a combination of urbanization and agriculture (FRAP 2003) and effects on biological systems of global warming are already evident (e.g. Inouye *et al*. 2000; Epps *et al*. 2004; Millar *et al*. 2004). Yet, many of the hotspots of recent evolution identified for mammals (Fig. 4) occur in relatively intact ecological landscapes. To protect interplay of selection and attenuated gene flow that promotes diversification (Endler 1977; Gavrilets 2003) will require protection of ecologically heterogeneous landscapes, with patch sizes that are at least an order of magnitude larger than per-generation dispersal distances of the taxa in question. The spatial scale of our results agrees with those of previous workers, emphasizing the large geographical scale needed to protect both isolated populations and especially to protect the sorts of environmental gradients we invoke as drivers of evolutionary processes (cf. Rouget *et al*. 2003). The geographical scope of this sort of conservation is beyond the scale any single agency or nongovernmental organization can administer. Already some 50% of California lands are federally managed (Fig. 4), but choosing which of those lands to closely protect and which new lands to protect requires careful coordination in conservation planning between agencies and a unified set of conservation priorities. To judge from these results for mammals, important areas in need of coordinated conservation effort include the Tehachapi Range, the Santa Lucia Range of the central coast, and areas along the northern coast of California (Fig. 4). The San Francisco Bay Area is similarly important, but the large urban population there serves to both prevent additional acquisition of natural land for conservation and an intense interest in conservation efforts in currently protected lands.

Another important aim for evolutionary conservation is to produce a quantitative model for evolutionary rates at the landscape scale, building on both the theoretical framework developed over 150 years of evolutionary thought and empirical observations of centres of rapid evolution (Fig. 1). Further development and validation of this model would allow conservation planners to translate geographical data about important environmental conditions (e.g. temperature or precipitation gradients, topographic or edaphic complexity, major boundaries between ecoregions, environmental stability) into maps that highlight areas with high diversity potential. Applying a model of DP to a range of scenarios of future climate and land use changes would allow policy makers to judge which areas could be relied upon to be consistently important for future biodiversity. In such a way, it will be possible to make evolutionary process part of the conservation policy toolkit, adding it as a complement to the existing approaches that prioritize protecting existing taxa and ecological communities.

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Appendix I

Subspecies data synopsis table. For each subspecies, the number of points used for modelling, AUC, Kappa, and area, are listed. N/A values for highly restricted ranges estimated by J.L.P. [1]Taxa which include environmental outliers to bolster sample size. In addition, presence and importance in subspecies endemism-richness hotspots are indicated ('–' indicates presence only, '+' indicates an important weighting)

Subspecies	*n*	AUC	Kappa	Area (km²)	North coast (N)	North coast (S)	SF Bay Area	Central coast	Central Valley	Tehachapis	Transverse Ranges	Owens Valley
Aplodontia rufa californica	27	0.92	0.80	26769								
Aplodontia rufa humboltiana	8	0.99	0.93	5682	+							
Aplodontia rufa phaea	11	0.99	0.99	1645			+					
Bassariscus astutus octavus[1]	4	0.81	0.61	20386							–	
Bassariscus astutus raptor	21	0.89	0.75	87826								
Canis latrans ochropus	102	0.75	0.41	172493	–	–	+	–	–	–	+	
Castor canadensis subauratus	17	0.99	0.97	18397					–		+	
Cervus elaphus nannodes	35	0.96	0.85	29814			–	–		–		–
Chaetodipus californicus bensoni	46	0.96	0.90	28532				+				
Chaetodipus californicus bernardinus	21	0.97	0.85	13552								
Chaetodipus californicus californicus	26	0.97	0.92	6546								
Chaetodipus californicus dispar	46	0.94	0.79	46448						+	–	
Chaetodipus californicus femoralis	23	0.97	0.93	22476								
Chaetodipus californicus marinensis	35	0.97	0.89	9793				+				
Chaetodipus californicus ochrus	66	0.97	0.87	36435						–		
Chaetodipus fallax pallidus	58	0.97	0.89	37639								
Chaetodipus penicillatus stephensi[1]	5	1.00	1.00	746								
Chaetodipus spinatus rufescens	25	0.98	0.87	41251							–	
Dipodomys agilis agilis	94	0.96	0.88	32200								
Dipodomys agilis cabezonae	31	0.98	0.89	13730							–	
Dipodomys agilis perplexus	36	0.98	0.87	43231						–	–	
Dipodomys californicus californicus	74	0.93	0.74	118785		–	–				–	
Dipodomys californicus eximius	5	0.99	0.99	5706							–	
Dipodomys californicus saxatilis	27	1.00	0.99	16474								
Dipodomys heermanni arenae	8	0.98	0.92	22327								
Dipodomys heermanni berkeleyensis	8	0.91	0.81	10181								
Dipodomys heermanni dixoni	7	0.99	0.99	1677					+			
Dipodomys heermanni goldmani	25	0.98	0.94	9945				+				
Dipodomys heermanni heermani	12	0.98	0.90	19119					–			
Dipodomys heermanni jolonensis	23	0.99	0.93	20801				+				
Dipodomys heermanni swarthi	24	0.98	0.90	14853								
Dipodomys heermanni tularensis	57	0.96	0.87	53566				+	–			
Dipodomys merriami collinus	13	0.99	0.95	7442								
Dipodomys merriami parvus	14	0.99	0.98	3141								
Dipodomys microps levipes	6	1.00	0.99	5368								+
Dipodomys microps microps	17	0.99	0.97	13578						–		+
Dipodomys nitratoides brevinasus	26	0.97	0.91	31283				+				
Dipodomys nitratoides exilis	N/A	N/A	N/A	314								
Dipodomys nitratoides nitratoides	25	0.99	0.97	12672								
Dipodomys panamintinus caudatus	12	1.00	1.00	3841								
Dipodomys panamintinus mohavensis	72	0.98	0.93	31923						–		–
Dipodomys panamintinus panamintinus	4	1.00	1.00	1076								+
Dipodomys venustus elephantinus	13	0.99	0.93	11549				+				

Appendix I *Continued*

Subspecies	*n*	AUC	Kappa	Area (km²)	North coast (N)	North coast (S)	SF Bay Area	Central coast	Central Valley	Tehachapis	Transverse Ranges	Owens Valley
Dipodomys venustus sanctiluciae	14	0.98	0.95	11405				+				
Dipodomys venustus venustus	18	0.98	0.91	7682				+				
Glaucomys sabrinus californicus[1]	8	0.98	0.88	18270								
Glaucomys sabrinus flaviventris	23	0.93	0.73	60037	–							
Glaucomys sabrinus lascivus	40	0.95	0.85	45417							–	
Glaucomys sabrinus stephensi[1]	5	0.82	0.61	33606	–	–	–					
Lepus americanus tahoensis	13	0.98	0.92	14318								
Lepus californicus bennettii	12	0.69	0.32	17124								
Lepus californicus californicus	89	0.81	0.51	150629	–	–	–	–	–			
Lepus californicus richardsonii	27	0.93	0.79	70648				–		–		
Lynx rufus californicus	149	0.77	0.41	93711		–	–	–		+		
Marmota flaviventris flaviventris	23	0.89	0.76	98433								
Marmota flaviventris sierrae	34	0.95	0.88	32044								
Martes americana humboltensis[1]	5	0.94	0.89	16468	–	–	–					
Martes americana sierrae	34	0.96	0.85	26017							–	
Mephitis mephitis holzneri	31	0.89	0.70	56177						–		
Microdipodops megacephalus polionotus	16	0.99	0.97	12882							+	
Microtus californicus aestuarinus	40	0.94	0.79	71405			–	–	–			
Microtus californicus californicus	113	0.94	0.80	24140				+			–	
Microtus californicus constrictus	15	0.97	0.87	12361	–	–						
Microtus californicus halophilus	10	1.00	0.99	317			+	–				
Microtus californicus kernensis	15	0.96	0.90	23114						+		
Microtus californicus mariposae	30	0.97	0.87	28254					–			
Microtus californicus sanctidiegi	75	0.93	0.78	59870						–		
Microtus californicus sanpabloensis	5	0.98	0.97	1687								
Microtus californicus vallicola	12	0.99	0.95	17058							–	–
Microtus longicaudus bernardinus	4	0.99	0.99	1009								
Microtus longicaudus sierrae	193	0.92	0.76	71806								
Mustela frenata latirostra	25	0.96	0.84	26298								
Mustela frenata munda	16	0.93	0.78	26354		–	–					
Mustela frenata nigriauris	63	0.94	0.79	27365				–			–	
Mustela frenata xanthogenys	17	0.99	0.96	25909					–			
Mustela vison aestuarina	36	0.77	0.46	69624	+	–	–	–	–			
Myotis yumanensis oxalis	9	0.90	0.80	35900					–			
Neotoma fuscipes annectens	44	0.94	0.84	16710				–				
Neotoma fuscipes bullatior	11	0.99	0.96	15514								
Neotoma fuscipes fuscipes	70	0.92	0.68	132141		–	–					
Neotoma fuscipes perplexa	27	0.96	0.83	25092				+				
Neotoma fuscipes riparia	N/A	N/A	N/A	27								
Perognathus alticolus alticolus	N/A	N/A	N/A	6								
Perognathus alticola inexpectatus[1]	5	1.00	1.00	2512						+		
Perognathus inornatus inornatus	54	0.93	0.81	79308			–		–	–		
Perognathus inornatus neglectus	12	0.91	0.74	78705					–	–		
Perognathus inornatus sillimani	N/A	N/A	N/A	829								
Peromyscus californicus benitoensis	21	0.97	0.89	25121			+	+				
Peromyscus californicus californicus	57	0.97	0.85	20598				+				
Peromyscus californicus insignis	110	0.94	0.81	57633						+		

Appendix I *Continued*

Subspecies	n	AUC	Kappa	Area (km^2)	North coast (N)	North coast (S)	SF Bay Area	Central coast	Central Valley	Tehachapis	Transverse Ranges	Owens Valley
Peromyscus californicus mariposae	13	0.96	0.87	12670						–		
Peromyscus californicus parasiticus	68	0.95	0.86	10334							–	
Reithrodontomys raviventris halicoetes	29	0.99	0.96	3797			+					
Reithrodontomys raviventris raviventris	22	0.98	0.96	3234								
Sorex ornatus californicus	69	0.91	0.71	50546			–	–	–			
Sorex ornatus ornatus	47	0.81	0.53	126055				–	–	–		–
Sorex ornatus relictus	N/A	N/A	N/A	856								
Sorex ornatus salarius[1]	5	1.00	1.00	16291			+				–	
Sorex ornatus salicornicus	N/A	N/A	N/A	404								
Sorex ornatus sinuosus	N/A	N/A	N/A	160								
Tamias amoenus monoensis	79	0.96	0.85	34393								
Tamias amoenus ochraceus	36	0.98	0.86	25950								
Tamias merriami kernensis	19	0.98	0.96	12449						–		–
Tamias merriami merriami	100	0.92	0.72	80436				–		–		
Tamias merriami pricei	30	0.98	0.90	8080				+				
Tamias panamintinus acrus[1]	5	1.00	1.00	898							–	
Tamias senex pacifica	24	0.99	0.92	16491	–							
Tamias sonomae alleni	25	0.97	0.85	5538		–	+					
Tamias sonomae sonomae	100	0.97	0.82	41933			–					
Tamias speciosus callipeplus	4	1.00	0.99	1637								
Tamias speciosus frater	159	0.95	0.83	26596								
Tamias speciosus sequoiensis	33	0.98	0.94	11208								
Tamias speciosus speciosus	22	0.99	0.92	6559								
Thomomys bottae albatus	46	1.00	0.98	28826								
Thomomys bottae alpinus	30	0.98	0.90	8781							–	
Thomomys bottae awahnee	15	0.98	0.92	10733								
Thomomys bottae bottae	448	0.82	0.54	132842			–	–		–		–
Thomomys bottae canus	7	1.00	1.00	2096								
Thomomys bottae laticeps	41	0.99	0.96	16477	–	–					–	
Thomomys bottae leucodon	18	0.99	0.95	15566								
Thomomys bottae mewa	44	0.98	0.91	27687					–			
Thomomys bottae navus	192	0.94	0.82	87735		–	–					
Thomomys bottae nigricans	79	0.96	0.88	29552								
Thomomys bottae operarius	8	1.00	1.00	1803								+
Thomomys bottae pascalis	40	0.99	0.94	31226							–	
Thomomys bottae perpallidus	173	0.98	0.90	145802						–		–
Thomomys bottae riparius	6	1.00	1.00	2529								
Thomomys bottae saxifragilis	66	0.99	0.98	15311							–	
Urocyon cinereoargenteus californicus	35	0.90	0.70	83378						–		
Vulpes macrotis mutica	201	0.99	0.93	24400								
Zapus princeps pacificus	107	0.91	0.73	106507							–	
Zapus trinotatus eureka	13	0.94	0.82	1280	+	+						
Zapus trinotatus orarius	6	1.00	0.98	1735			+					
Total '+'					3	1	8	14	1	5	3	4
Total taxa					11	14	23	28	16	23	23	11
+/total					0.272727273	0.071428571	0.347826087	0.5	0.0625	0.217391304	0.130434783	0.363636364

Appendix II

Importance of mammal species to hotspots. '-' indicates presence in the hotspots of that area, but low weighting in endemism-richness and neo-endemism richness analyses. 'ER' indicates a high weighting in the endemism-richness analysis. 'NE' indicates a high weighting in the neo-endemism and neo-endemism richness analyses

Family	Scientific name	North Coast	SF Bay Area	Central Coast/ southern Coast Rages/ SW San Joaquin Valley	Tehachapi Range	Transverse Ranges	Peninsular Ranges	Southern Sierra Nevada	Central Sierra Nevada
Soricidae	*Sorex lyelli*								ER, NE
Soricidae	*Sorex ornatus*		—	—	—	—	—	—	—
Geomyidae	*Thomomys monticola*								—
Heteromyidae	*Chaetodipus californicus*		—	—	—	—	—	—	
Heteromyidae	*Dipodomys agilis*				NE	NE	NE	NE	
Heteromyidae	*Dipodomys californicus*	ER							
Heteromyidae	*Dipodomys heermanni*		NE	NE					
Heteromyidae	*Dipodomys ingens*			ER					
Heteromyidae	*Dipodomys nitratoides*			ER					
Heteromyidae	*Dipodomys panamintus*				NE	NE		NE	
Heteromyidae	*Dipodomys stephensi*						ER, NE		
Heteromyidae	*Dipodomys venustus*		—	—					
Heteromyidae	*Perognathus alticolus*				ER, NE	ER, NE (extirpated)			
Heteromyidae	*Perognathus inornatus*			—				—	
Muridae	*Arborimus pomo*	ER, NE							
Muridae	*Microtus californicus*	—	—	—	—	—	—	—	—
Muridae	*Neotoma fuscipes*	—	—	—					
Muridae	*Peromyscus californicus*		—	—	—	—	—	—	
Muridae	*Reithrodontomys raviventris*		ER						
Sciuridae	*Ammospermophilus nelsoni*			ER					
Sciuridae	*Spermophilus mojavensis*							NE	
Sciuridae	*Tamias alpinus*								ER, NE
Sciuridae	*Tamias merriami*			NE	NE	NE	NE	NE	—
Sciuridae	*Tamias ochrogenys*	ER, NE							
Sciuridae	*Tamias quadrimaculatus*								—
Sciuridae	*Tamias senex*								—
Sciuridae	*Tamias sonomae*	ER	—						
Sciuridae	*Tamias speciosus*					NE			NE