Phylogenetic perspectives on Californian plant diversity, endemism, and conservation
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California Floristic Province

Global-scale biodiversity hotspot (~300,000 km$^2$)

Isolated, young Mediterranean-type climate (winter wet / summer dry)

Geological & climatic diversity & dynamism

Pockets of stable, equable climate (refugia)

Figure from Raven & Axelrod 1978
Discoveries in California floristics

- Fine-scale diversity worthy of taxonomic recognition and informative about evolution keeps emerging
- Progress in understanding origins and relationships of CA flora deepens appreciation for magnitude of diversification in CA (& N.Am.)
- New approaches to studying spatial patterns of diversity and endemism help to pinpoint areas of special floristic and conservation value
Undiscovered fine-scale plant diversity in California?


Shasta snow-wreath (*Neviusia cliftonii*)
Discovered in 1992 in N. California

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More discoveries in the Klamath Ranges

Vaccinium shastense subsp. shastense

Adiantum shastense

Erythronium shastense

© Len Lindstrand III

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The *Navarretia intertexta* complex (Johnson et al. 2013 *Phytotaxa*)
New & Revived Diversity in Monkeyflowers
(see Fraga’s revised Phrymaceae, Jepson eFlora)

*Erythranthe montioides* complex

*Erythranthe palmeri* complex

sensu Thompson (2012)

- Newly described species
- Resurrected species
Collinsia “metamorphica” complex
endemic to upper Merced River drainage
(Baldwin et al. 2011 Amer. J. Bot.; M.S. Park et al., in prep.)
Host-specific cryptic diversity in North American broomrapes

Aphyllon sect. Aphyllon (Orobanchaceae)

Aphyllon clades (by host)

A. fasciculatum
- Artemisia
- Eriogonum, Eriophyllum, or Hydrophyllaceae
- Galium = A. epigalium sp. nov.

A. purpureum
- Apioidae
- Asteraceae
- Saxifragales

A. uniflorum
- Asteraceae

Aphyllon epigalium, a new species

Colwell et al. 2017
Madroño 64:99-107

A novel example of horizontal gene transfer, from Galium to Aphyllon
(Schneider et al. 2018 Proc. R. Soc. B)
A discovery anticipated 100 yrs earlier

“This has the habit of *O. uniflora* but the calyx-segments are broad as in *O. fasciculata*. Moreover the color of the flowers is yellow as per note in field book, no. 6385. A spec. similar to this, Comptche, Harriet Walker 368, is in U.C. Herb.”

– W. L. Jepson July, 1918
And (semi-)cryptic tarplants in these taxa

- **Centromadia parryi** subsp. congdonii
- **Layia gaillardioides**
- **Blepharizonia plumosa**
- **Calycadenia pauciflora** race ramulos
- **Carlquistia muirii**
Heliothinae moths: 20 known tarweed specialists (in larval stage) discovered by Terry Sears
Cryptic lineage of “Megaprotubera” on cryptic lineage of Calycadenia multiglandulosa
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Comprehensive review on assembly and evolution of California’s vascular flora in 1978
CA-FP taxa of Leguminosae that belong to larger, primarily North American radiations based on recent phylogenetic evidence.

**Lupinus** (Genisteae)  
Drummond 2008  

**Astragalus** (Galegeae)  
Wojciechowski et al. 1999  
*Syst. Bot.*

**Tribe Psoraleeae**  
Egan & Crandall 2008  
*BMC Biol.*

**Lathyrus** (Fabeae)  
© Barry Breckling

**Trifolium** (Trifolieae)  
Ellison et al. 2006  

**Tribe Loteae**  
Allan & Porter 2000  
*Amer. J. Bot.*
CA-FP taxa of Compositae that belong to larger, primarily North American radiations based on recent phylogenetic evidence.

*Cirsium* (Cardueae)  
Kelch & Baldwin 2003  
*Mol, Ecol.*

Most native Astereae

Native Filaginiae (Gnaphalieae)

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Noyes & Rieseberg 1999  
*Amer. J. Bot.*

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Galbany-Casals et al. 2010  
*Taxon*

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Primarily western North American genera of Senecioneae

Lee et al. 2003  
*Syst. Bot.*

Primarily North American genera of Cichorieae

Pelser et al. 2010  
*Amer. J. Bot.*
Extreme dysploid chromosome number reduction in resurrected & expanded tribe Madieae
Mediterranean-Californian disjunctions mostly explained by long-distance dispersal & ecological convergence (Kadereit & Baldwin 2012 *Taxon*).

Limited long-distance dispersal resolved for the Californian flora (Wen & Ickert-Bond 2009 *J Syst Evol*; Kadereit & Baldwin 2012 *Taxon*), mostly out (especially to Chile); arguably most significant for the Hawaiian flora...
California tarweeds (subtribe Madiinae; Compositae)
The Hawaiian silversword alliance (Argyrogedium, Dubautia, Wilkesia) descended from Calif. tarweeds (Baldwin et al. 1991 PNAS; Barrier et al. 1999 Mol Biol Evol)
Some other major Hawaiian endemic clades nested in western North American grades

(Sanicula (Apiaceae) Vargas et al. 1998 PNAS)

Hawaiian mints

Lindquist & Albert 2002 Amer J Bot

Hawaiian and American Viola

Ballard & Sytsma 2000 Evolution;
Marcussen et al. 2012 Syst Biol
Endemic (or near endemic) CA-FP conifers confirmed as ancient

- *Abies bracteata*
- *Picea breweriana*
- *Calocedrus decurrens*

References:
- Xiang et al. 2009 *Taxon*
- Bouille et al. 2011 *Tree Genet. Genomes*
Ancient, xeric-adapted (or -preadapted) woody endemic CA-FP eudicots

Aesculus californica (Sapindaceae)

Lyonothamnus (Rosaceae)

Carpenteria (Hydrangeaceae)

Malosma (Anacardiaceae)

Pickeringia (Fabaceae)

Cneoridium (Rutaceae)
Hesperelaea (Oleaceae): Isla Guadalupe endemic genus, extinct in 1800s'
cpDNA & nrDNA sequenced using NGS

Lineage older than Isla Guadalupe; clade includes New World genera
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The California Plant Phylodiversity Project
A specimen-based, taxonomically comprehensive reanalysis of spatial diversity patterns

Baldwin et al. (2017)
Species richness and endemism in the native flora of California.
*Amer. J. Bot.* 104:487-501

993 genera, 5255 species of Californian vascular plants

Two main *Biodiverse* analyses:
All native vascular plants
All natives restricted to California

We compared the main centers of endemism discovered using range-weighted (RW) & non-RW turnover

1.38 million georeferenced specimen records (including non-CCH records)
Spatial measures of species richness & endemism

- **Species richness (SR):** Number of spp./grid cell
- **Weighted endemism (WE):** Inverse weighting of spp. by range size
- **Corrected weighted endemism (CWE):** WE/SR (WE corrected for species richness)
- **Significant endemism (Rand END):** A cell with endemism value in top 5% of the distribution of random values, from spatial randomization
Areas of both high richness & endemism

Klamath Ranges (high)  Mt. Shasta region  Sierra Nevada crest

White & Inyo Range  Sweetwater Mountains

San Bernardino Mountains (high)  Santa Rosa Mtns
Areas of both high richness & endemism

New York Mountains

Panamint Mountains

Clark Mountain Range

Providence Mountains

Desert Mountains of the Mojave Desert: Significant endemism even for species restricted to CA
Low richness but high endemism

The Channel Islands: A high proportion of range-restricted species but relatively modest overall species diversity
Local endemism hotspots

- Previously proposed endemic areas of Central Coast Ranges among areas of high weighted endemism (WE)
- Some also with significant endemism (Hamilton, Monterey, Napa-Lake, Pitkin-Bodega, San Carlos)
- Other areas (e.g., San Francisco Peninsula) also with significantly high endemism

Stebbins & Major (1965) *Ecol Monogr*
Range-weighted turnover among significant centers of species endemism

Jepson Bioregions
The Jepson eFlora:
http://ucjeps.berkeley.edu/eflora/
What is biodiversity?

Species richness

Phylogenetic diversity

3 species

7 My

20 My
Phyloendemism (range-weighted phylodiversity) patterns indicate concentrated centers of significantly high endemism in drier regions.

Thornhill et al. (2017) *BMC Biology*
Where are the priority conservation areas based on different biodiversity measures?

Kling et al. (2019)  
*Phil. Trans. R. Soc. B*
Optimal conservation targets:

- Poorly protected
- Many resident taxa with:
  - Long branches
  - Small ranges
  - Poor protection across ranges
Top conservation priorities
Consensus areas of high conservation priority across different biodiversity facets
California Plant Phylodiversity Atlas (designed by M. Kling): A new conservation & floristic resource of the CPPP (JEPS)
Conclusions about CA flora

• Estimates of CA-FP diversity & diversification continue to rise, underscoring CA-FP as a biodiversity hotspot

• Relative importance of factors contributing to richness & endemism still uncertain but most endemic CA-FP lineages post-date mid-Miocene shift toward summer-drought

• High floristic richness strongly associated with areas of high topographic & substrate heterogeneity in the CA-FP

• Significantly high endemism (higher than expected based on levels of richness) especially notable in drier regions

• Areas of highest conservation priority largely in CA-FP foothills and coastal regions, where development likely
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A general finding for Eurasian-North American disjunctions: west. N. Amer. taxa usually most closely related to east. N. Amer. taxa

Donoghue & Smith 2004
*Phil. Trans. R. Soc. Lond. B*

Wen et al. 2010 *Darwin’s Heritage Today*

\[ C_j = \sum_{i=1}^{n} \frac{p_{ij} s_i}{R_j} \]

- **Sum across grid cells**
- **Clade presence probability**
- **Cell protection status**
- **Clade range size**
- **Clade conservation status**
Optimal conservation targets:

• Poorly protected
• Many resident taxa with:
  • Long branches
  • Small ranges
  • Poor protection across ranges

Stepwise optimization algorithm:

1. Calculate the marginal value of fully protecting each site
2. Mark highest-value site as protected
3. Rinse & repeat
Total marginal benefit of fully protecting site

\[ MV_i = \sum_{j=1}^{n} u_j \cdot \Delta B \]

- Sum across clades
- Branch segment length
- Security boost to clade from fully protecting site
Stepwise optimization algorithm:

1. Calculate the marginal value of fully protecting each site
2. Mark highest-value site as protected
3. Rinse & repeat

\[ MV_i = \sum_{j=1}^{n} v_j \Delta B \]