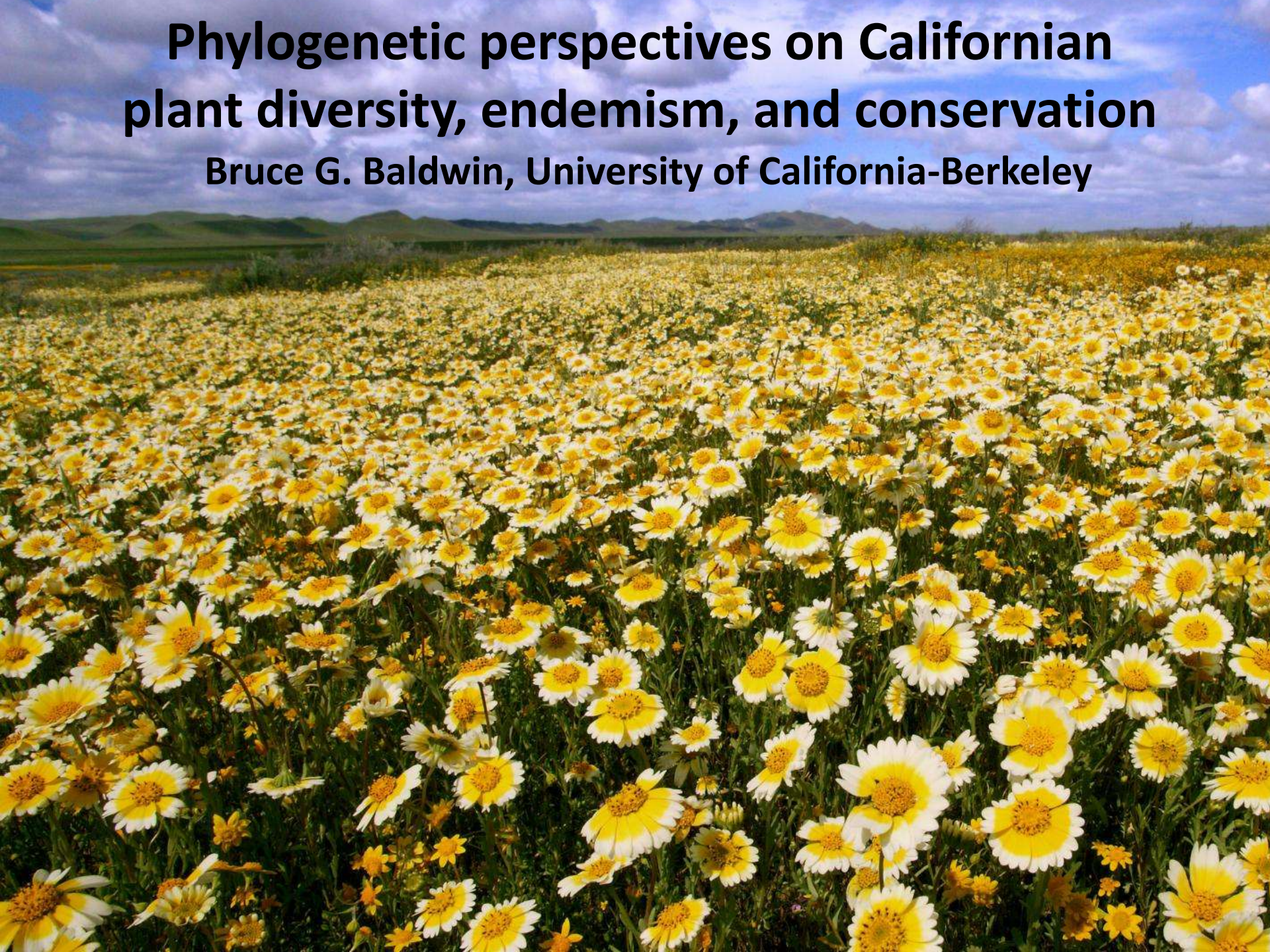
Phylogenetic perspectives on Californian plant diversity, endemism, and conservation

Bruce G. Baldwin, University of California-Berkeley



California Floristic Province

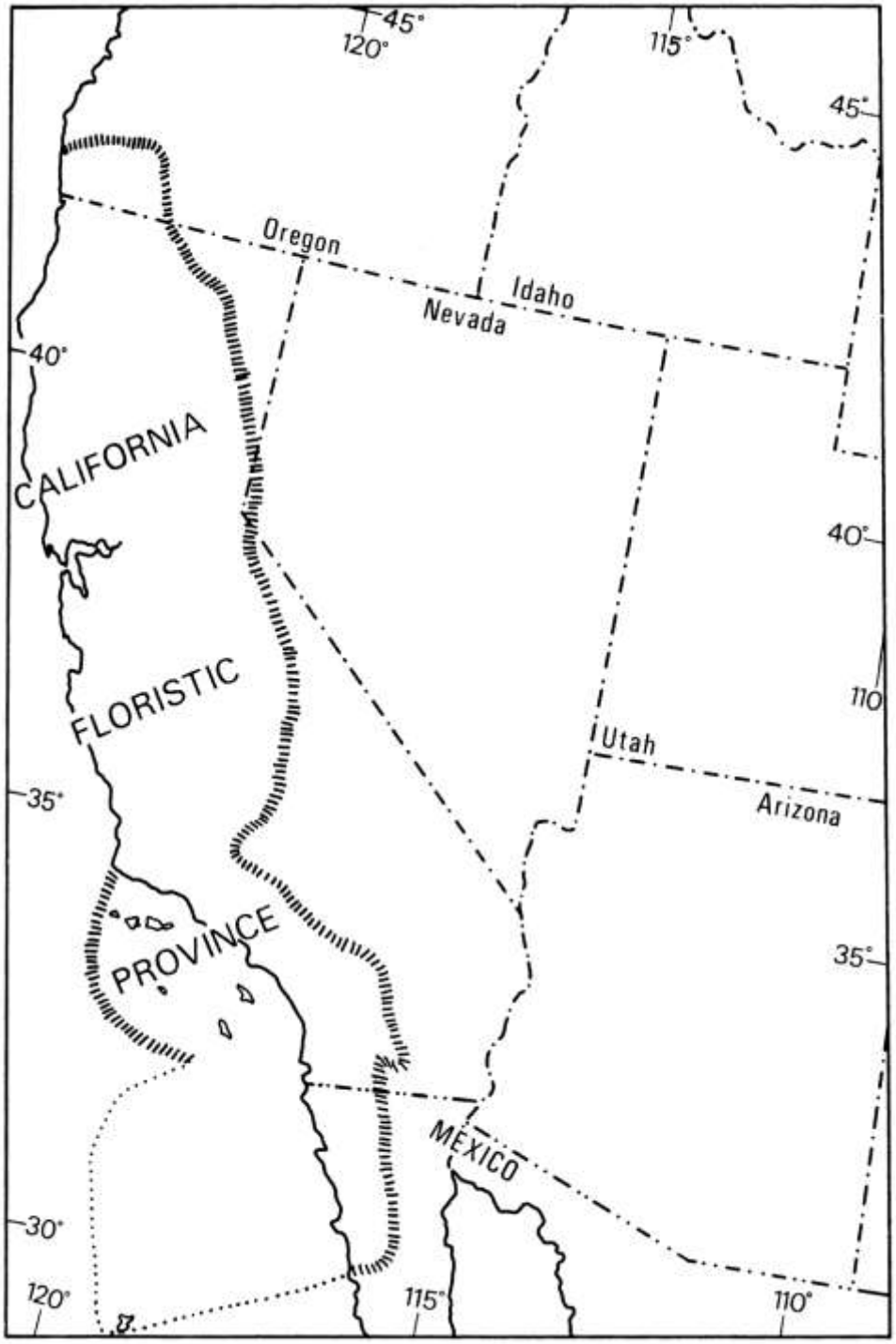
Global-scale biodiversity hotspot
(~300,000 km^2)

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

Geological & climatic diversity & dynamism

Pockets of stable, equable climate (refugia)

Figure from Raven & Axelrod 1978

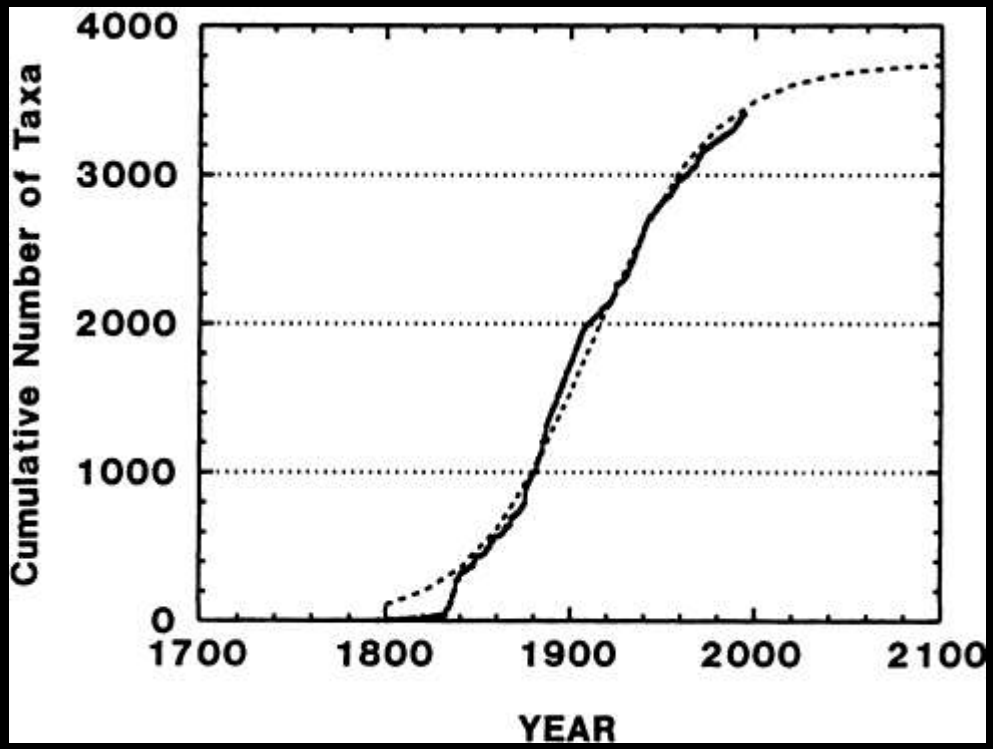


Discoveries in California floristics

- 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



Historical trend in accumulation of endemic vascular plant taxa in California until 1993 (dark line) and future projection (dashed line) (D. Taylor *in* Ertter 2000 *Ann. Missouri Bot. Gard.*)

More discoveries in e Klamath Ranges

Vaccinium shastense subsp. *shastense*

Adiantum shastense

Erythronium shastense

The *Navarretia intertexta* complex (Johnson et al. 2013 *Phytotaxa*)

Navarretia saximontana
4n

Navarretia propinqua
4n

Navarretia intertexta
2n

Navarretia furnissii
2n

Navarretia paradoxiclara
2n

Navarretia paradoxinota
2n

New & Revived Diversity in Monkeyflowers
(see Fraga's revised Phrymaceae, Jepson eFlora)

***Erythranthe montioides* complex**

sensu Thompson (2012)

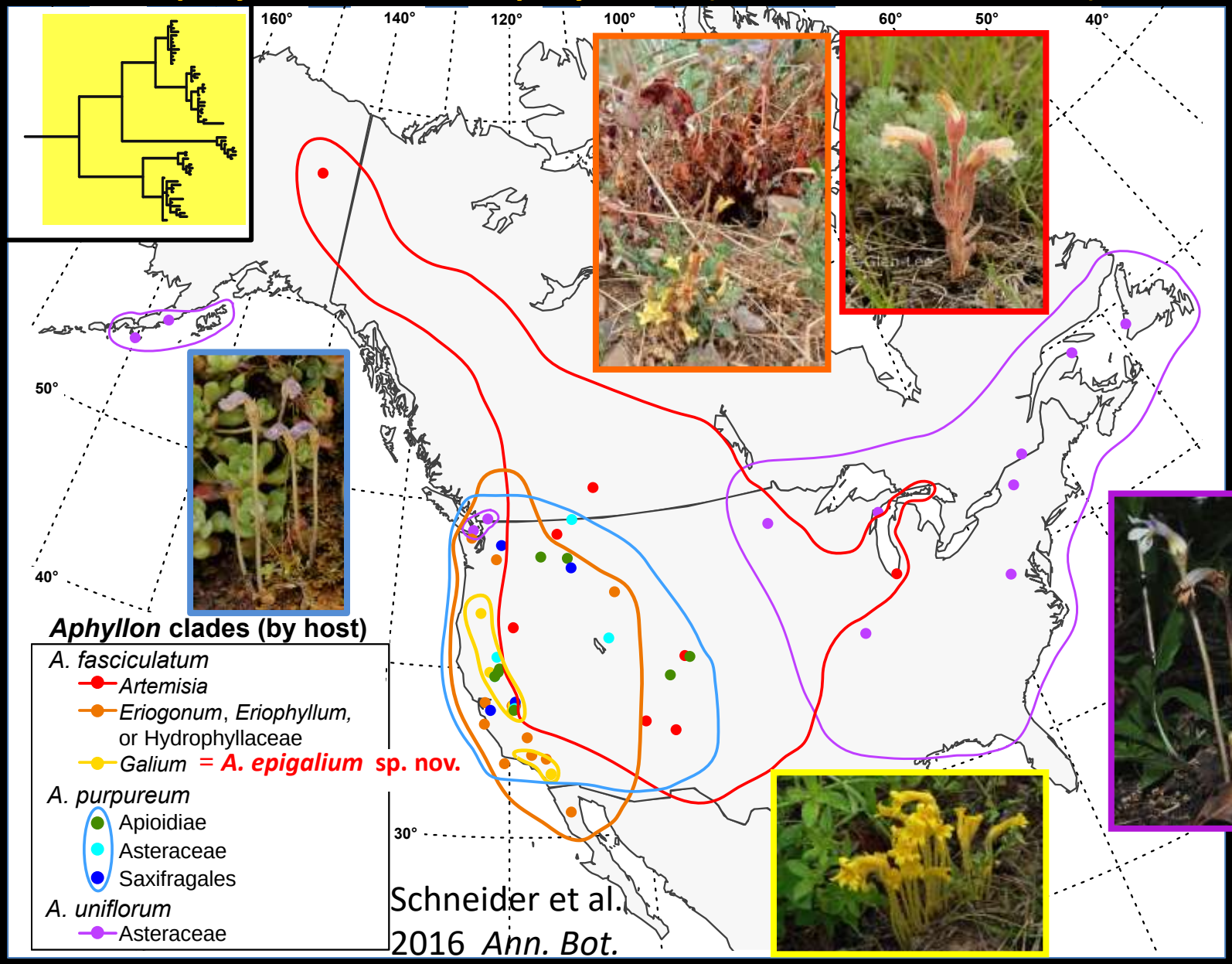
***Erythranthe palmeri* complex**

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.)

Aphyllon sect. *Aphyllon* (Orobanchaceae)



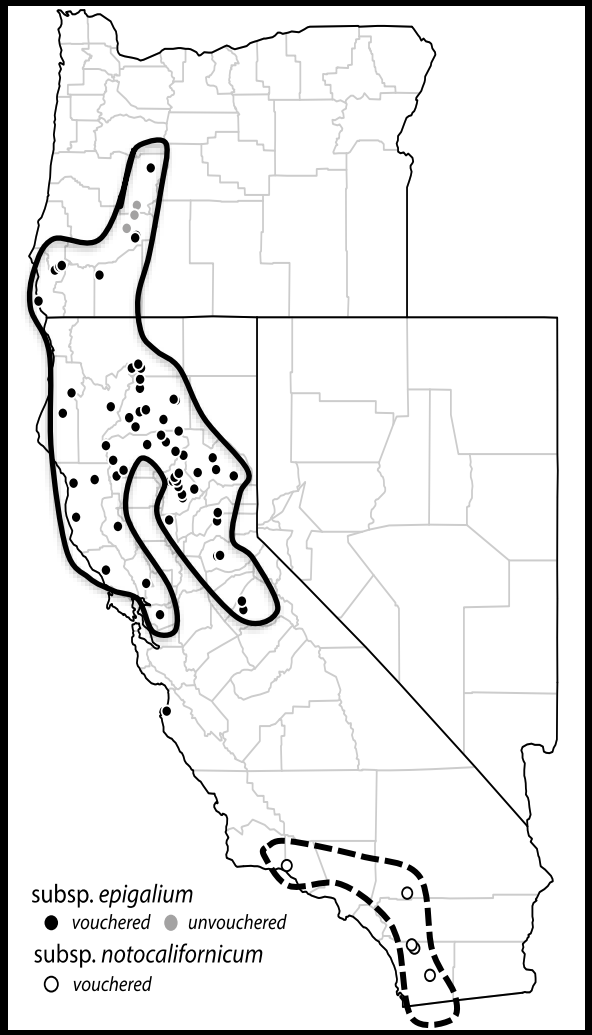
Host-specific cryptic diversity in North American broomrapes

Aphyllon epigalium, a new species

subsp. *epigalium*

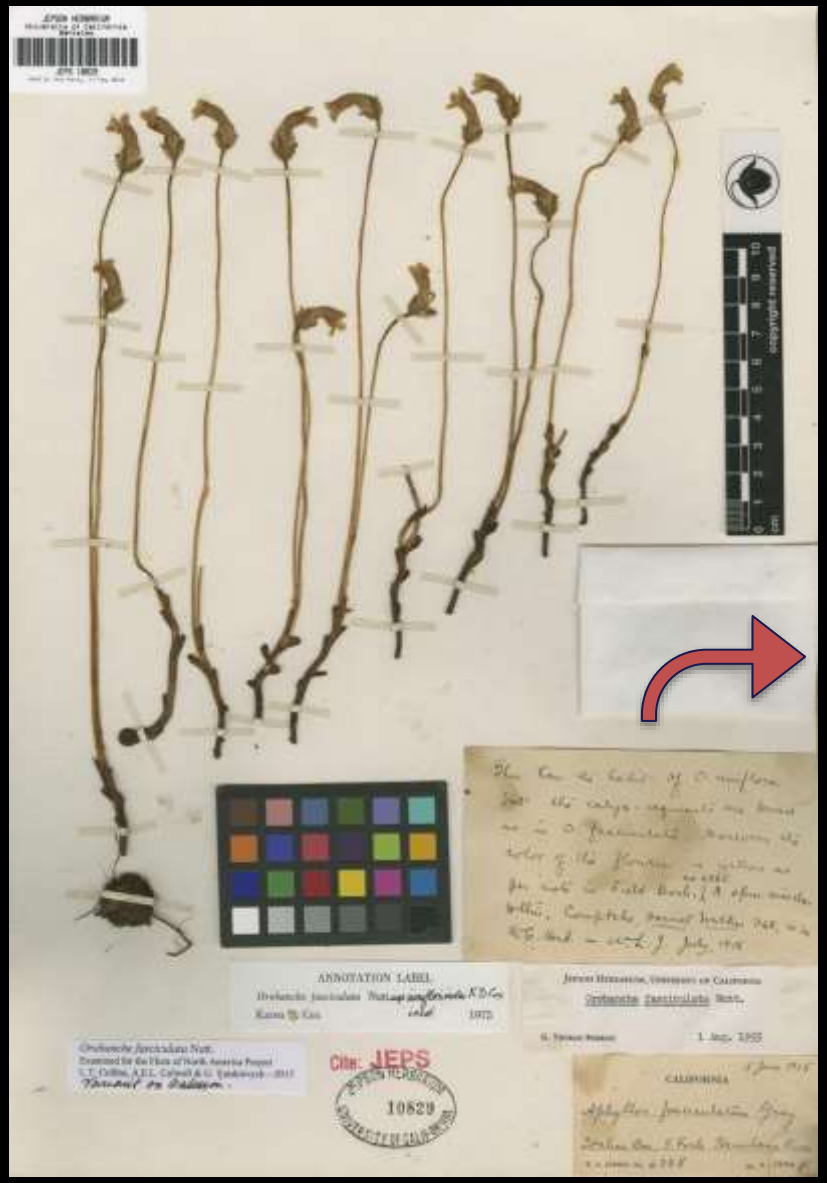
subsp. *notocalifornicum*

Colwell et al. 2017
Madroño 64:99-107



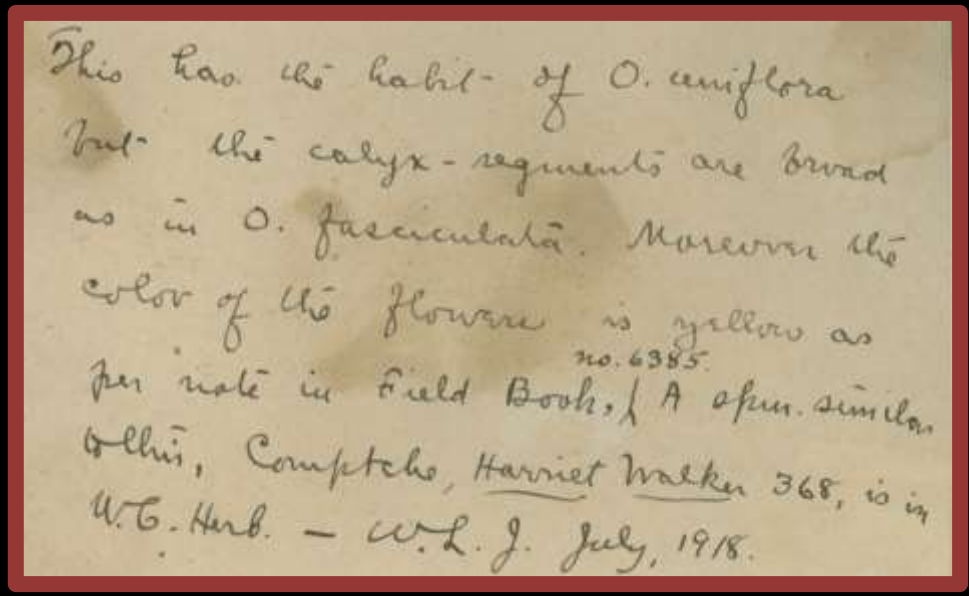
A novel example of horizontal gene transfer, from *Galium* to *Aphyllon* (Schneider et al. 2018 *Proc. R. Soc. B*)

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."

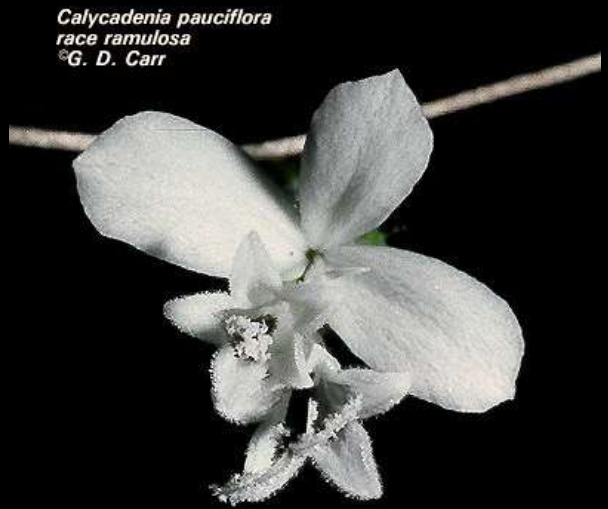
– W. L. Jepson July, 1918



And (semi-)cryptic tarplants in these taxa

Centromadia parryi subsp. *congdonii*

Layia gaillardioides



Calycadenia pauciflora

Madia sativa

Blepharizonia plumosa

Carlquistia muirii

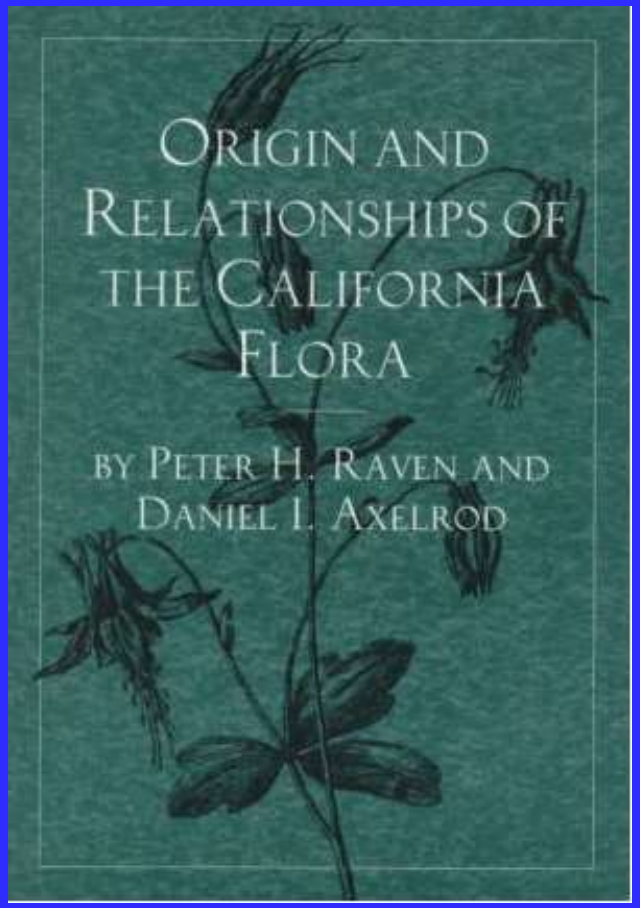
Heliothinae moths:
20 known tarweed specialists (in larval stage) discovered by Terry Sears

Cryptic lineage of *"*Megaprotubera*"* on cryptic lineage of *Calycadenia multiglandulosa*

Discoveries in California floristics

- Fine-scale diversity worthy of taxonomic recognition and informative about evolution keeps emerging from systematic studies
- 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

Peter H. Raven

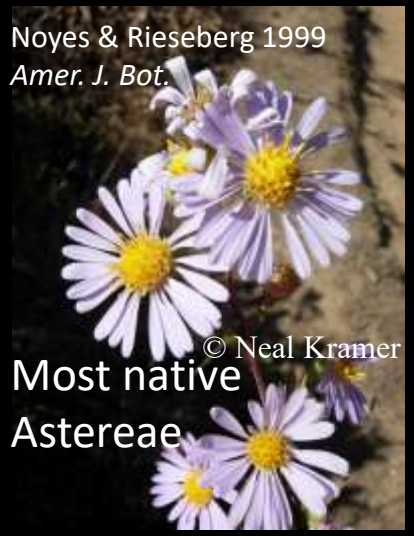


Daniel I. Axelrod

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

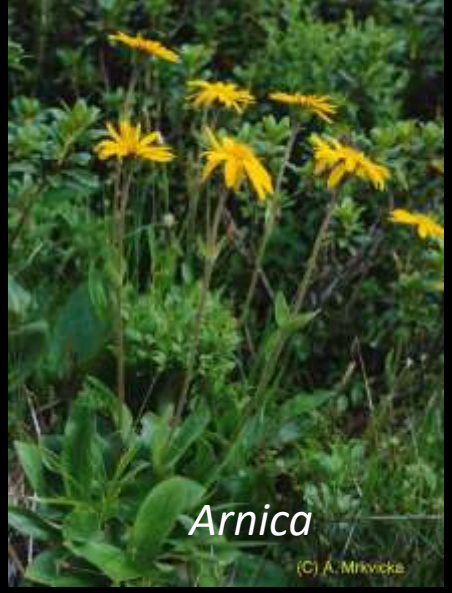
CA-FP taxa of Compositae that belong to larger, primarily North American radiations based on recent phylogenetic evidence



x=19 Hulseinae

x=19 *Venegasia*

Venegasiinae



x = 19 Arnicinae

x = 17 Madiinae

n = 4

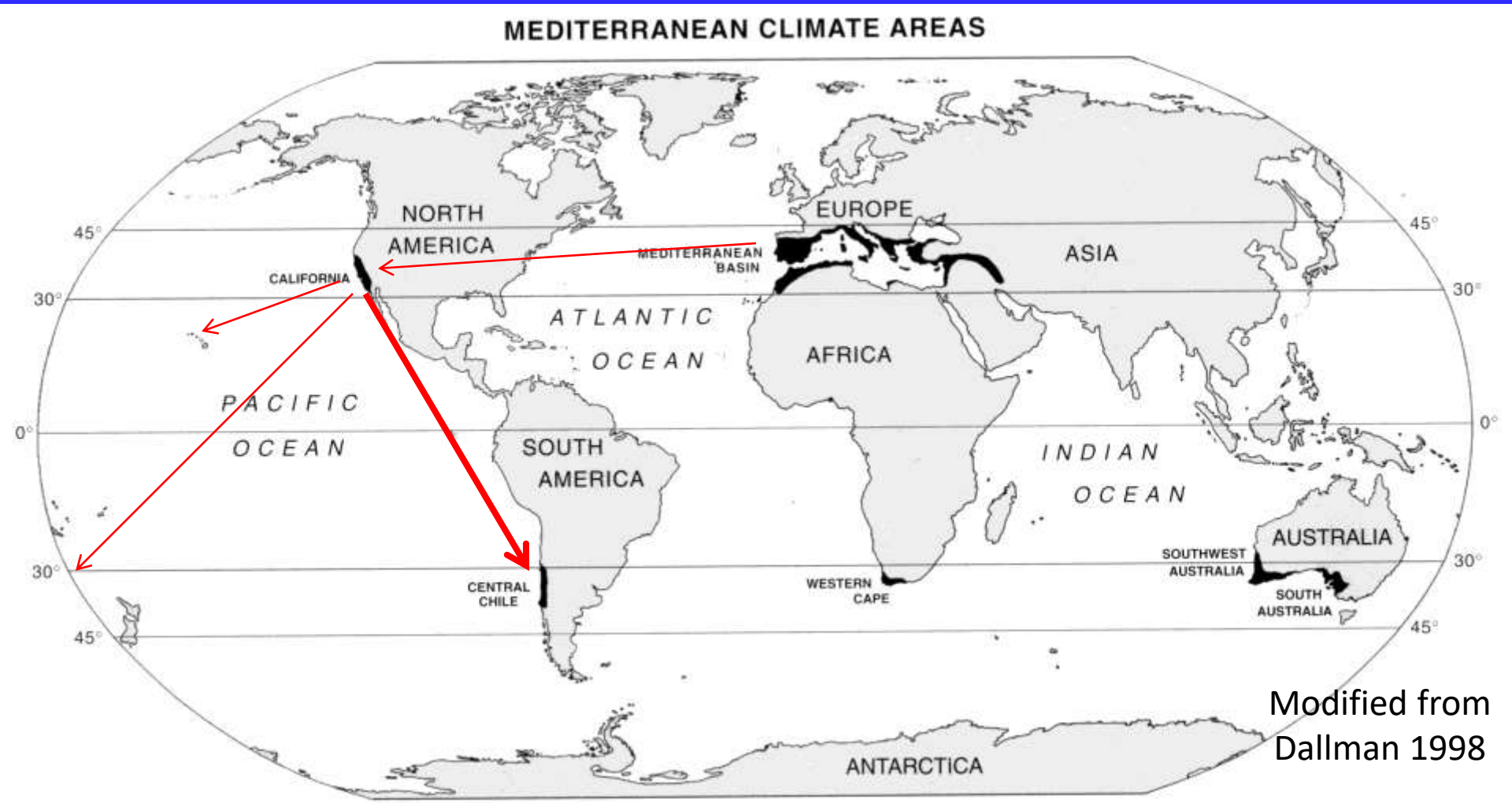
x = 19 Baeriinae (*Constancea*)

x = 8 clades

n = 3

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*)



Modified from Dallman 1998

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 (*Argyroxiphium, Dubautia, Wilkesia*) descended from Calif. tarweeds (Baldwin et al. 1991 *PNAS*; Barrier et al. 1999 *Mol Biol Evol*)

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

Lindquist & Albert 2002 *Amer J Bot*

Hawaiian mints

Californian *Stachys*

Some other major Hawaiian endemic clades nested in western North American grades

(Baldwin & Wagner 2010 *Ann. 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


Charles Webber © CAS

Xiang et al. 2009 *Taxon*;
Aguirre-Planter et al. 2012
Mol. Phylogenet. Evol.

© Steven Harper

Abies bracteata


© Timothy D. Ives

Bouille et al. 2011
Tree Genet. Genomes

© Neal Kramer

Picea breweriana

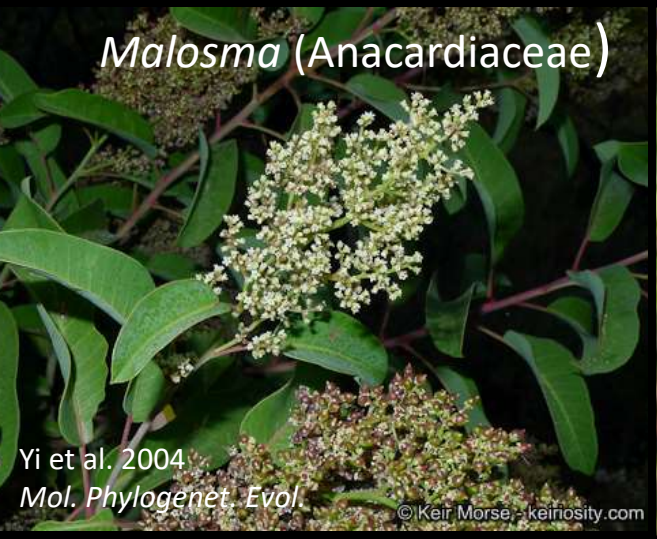

© Julie Kierstead Nelson

Chen et al. 2009
Bot. Stud.

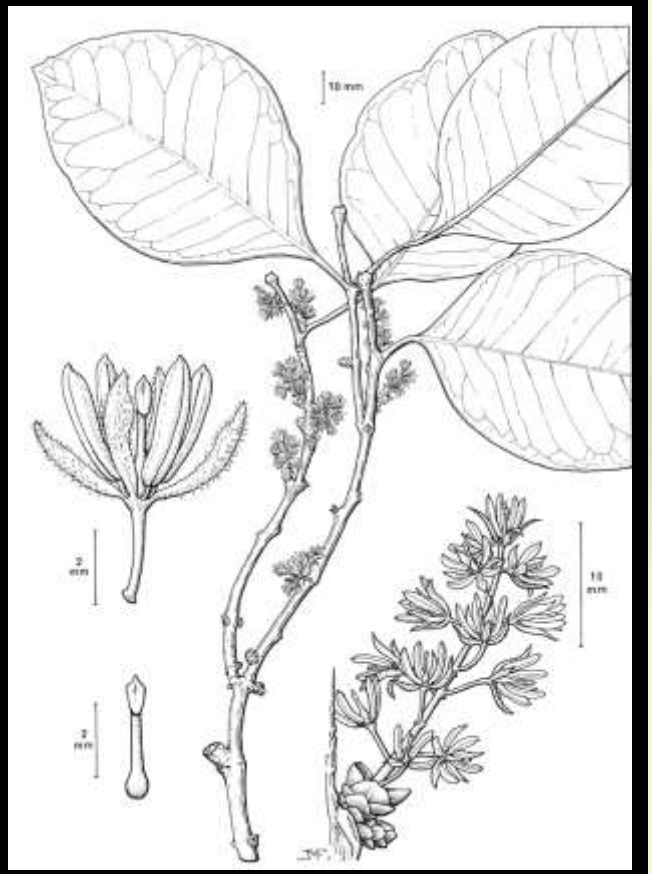
Calocedrus decurrens

© Ryan Gilmore

Ancient, xeric-adapted (or -preapted) woody endemic CA-FP eudicots



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



Priogymnanthus hasslerianus

Hesperelaea palmeri

Forestiera pubescens

Lineage older than Isla Guadalupe; clade includes New World genera
Forestiera & *Priogymnanthus* (Zedane et al. 2016 *Biol. J. Linn. Soc*)

Discoveries in California floristics

- Fine-scale diversity worthy of taxonomic recognition and informative about evolution keeps emerging from systematic studies
- 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

The California Plant Phylodiversity Project

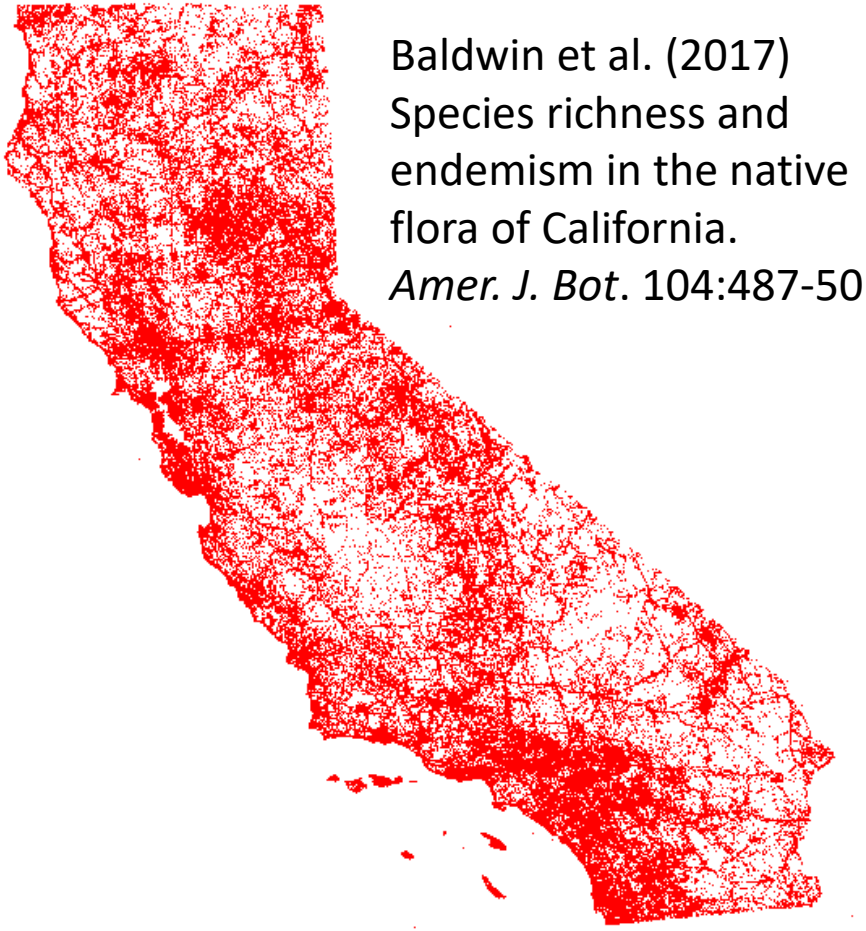
A specimen-based, taxonomically comprehensive reanalysis of spatial diversity patterns

Consortium of California Herbaria

http://ucjeps.berkeley.edu/consortium/

Jepson eFlora

993 genera, 5255 species of Californian vascular plants



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

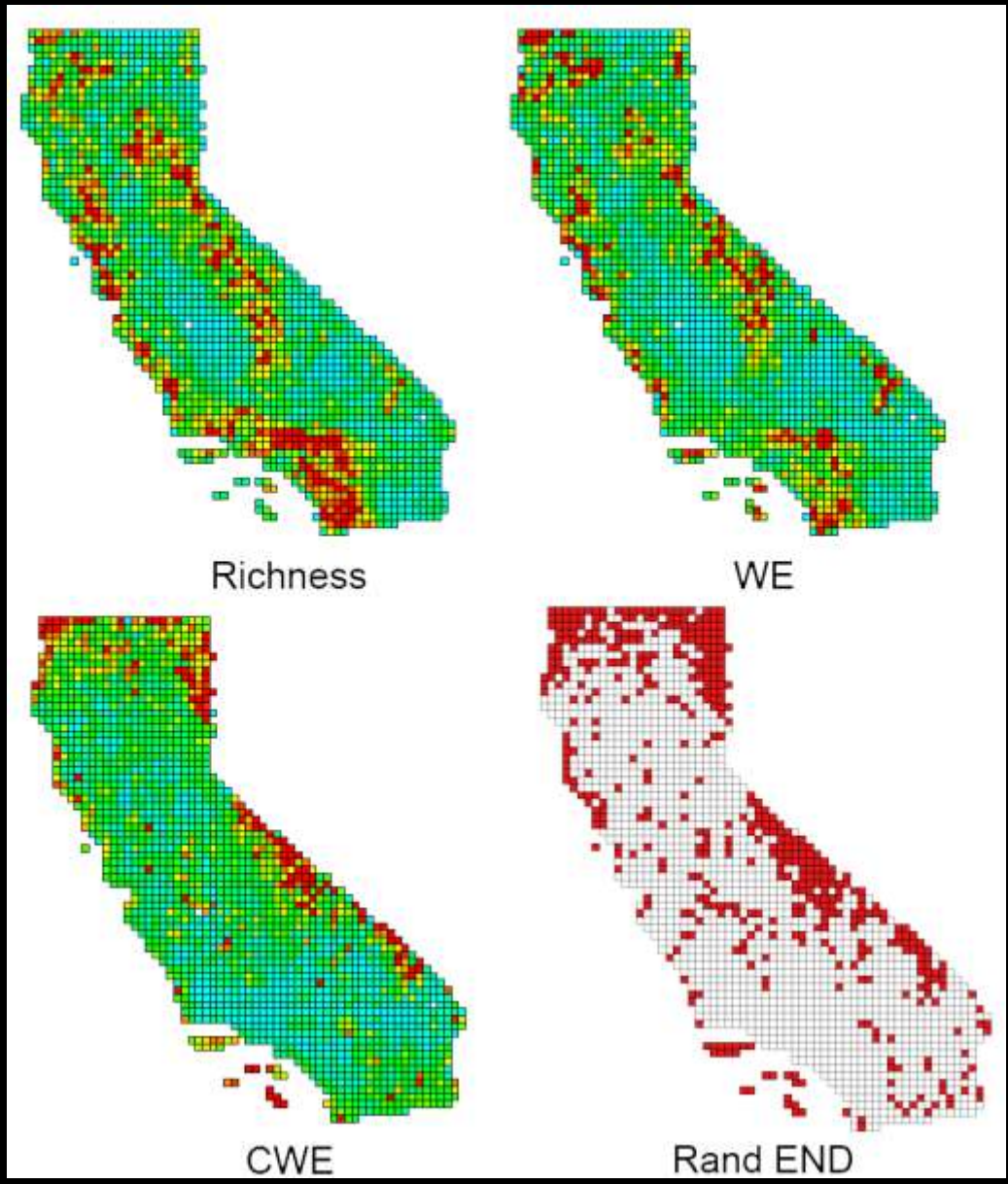
Two main *Biodiverse* analyses:
All native vascular plants
All natives restricted to California

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

Areas of both high richness & endemism


New York Mountains


Panamint Mountains


Clark Mountain Range


Providence Mountains

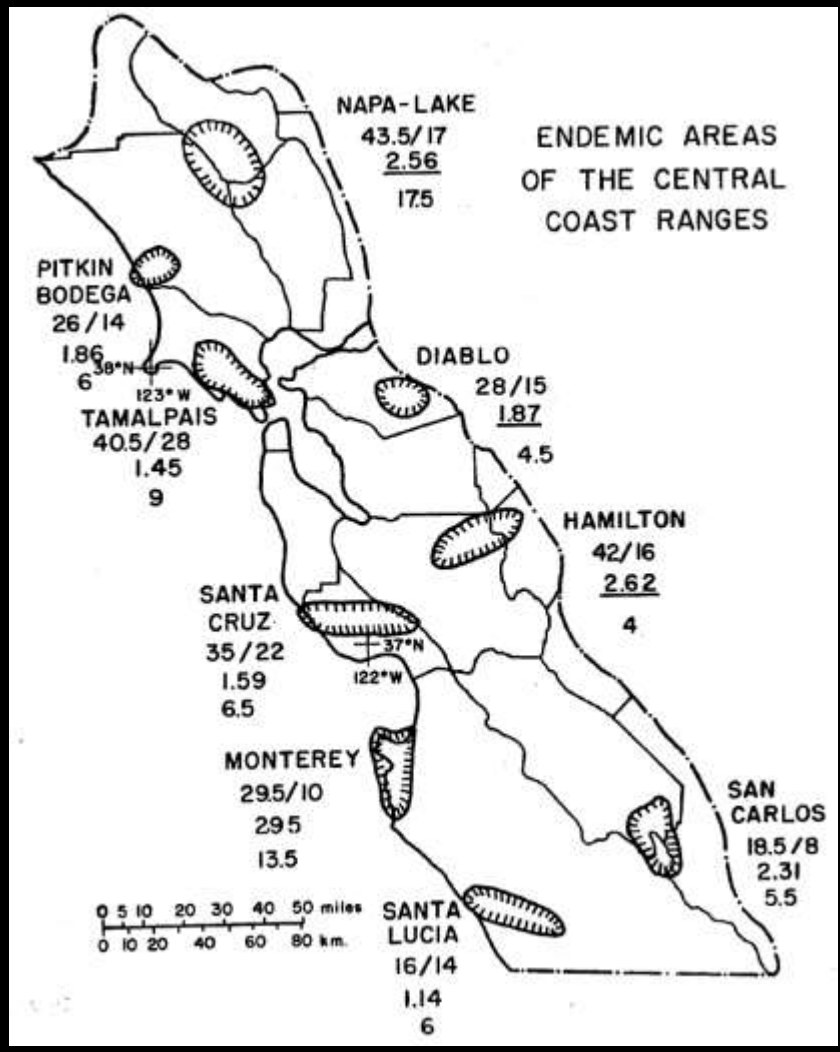
Desert Mountains of the Mojave Desert: Significant endemism even for species restricted to CA

Low richness but high endemism

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

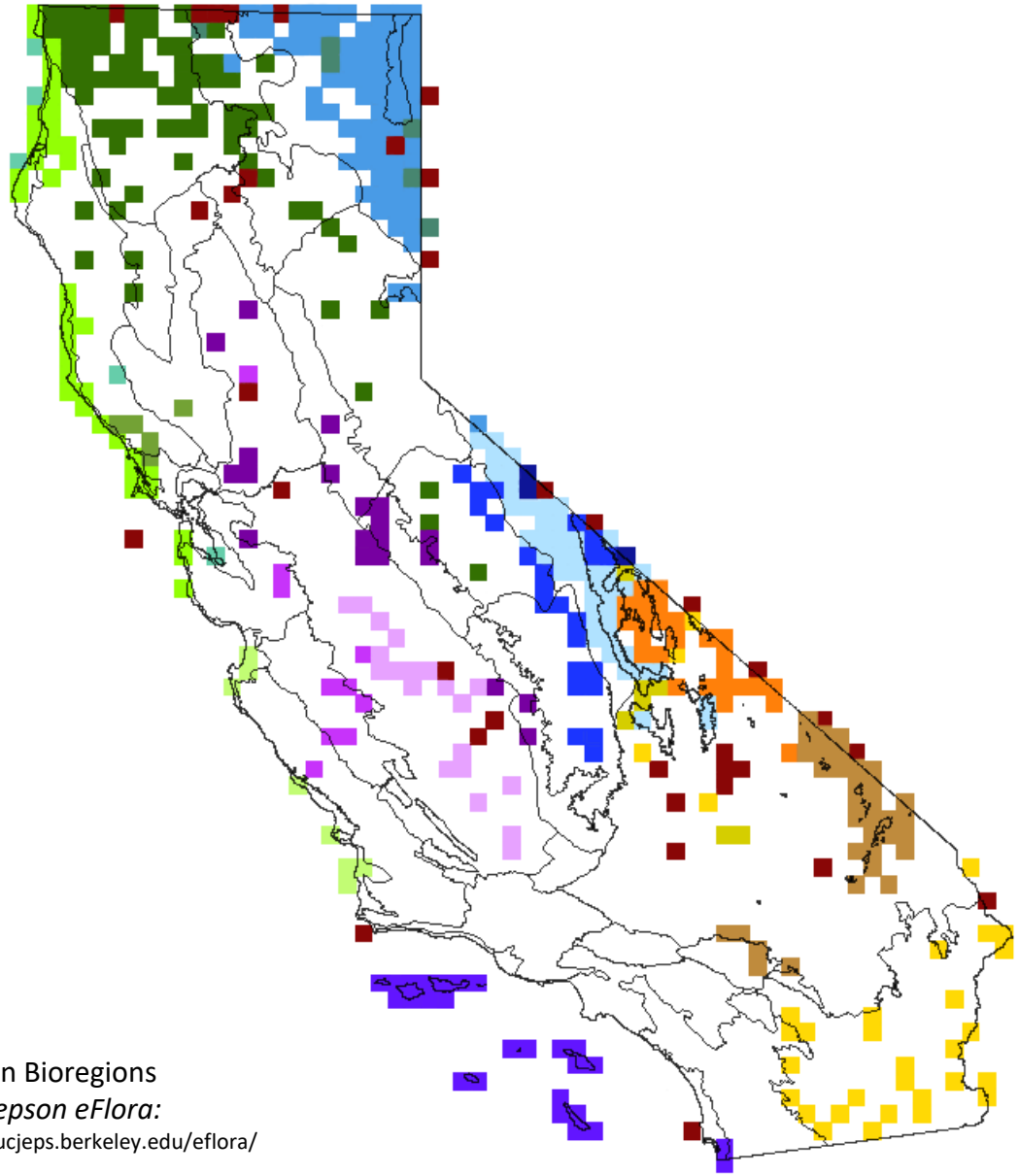
Local endemism hotspots

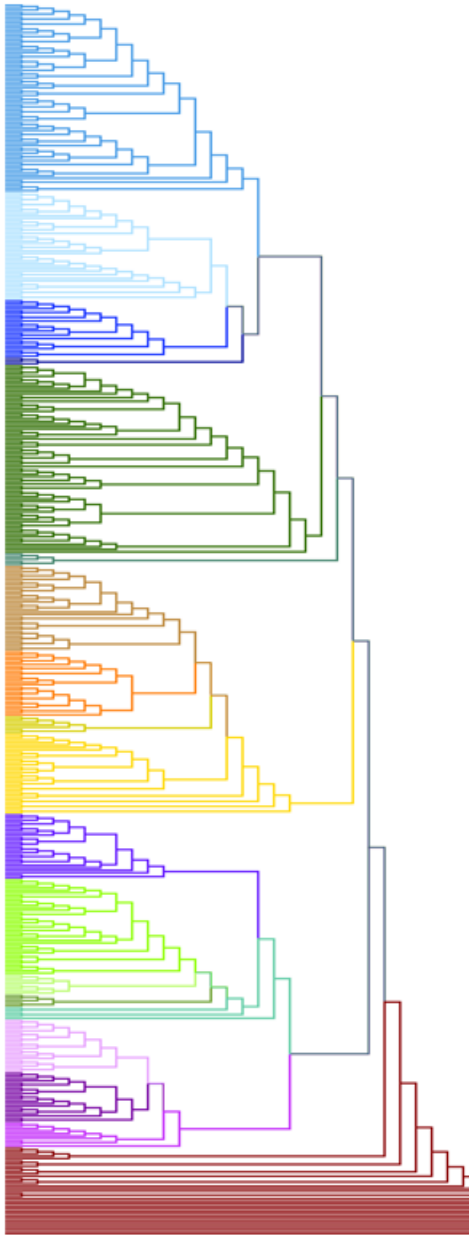
- Previously proposed endemic areas of Central Coast Ranges among areas of high weighted endemism (WE)
- Some also with significant endemism (Hamilton, Monterey, Napa-Lake, Pitkin-Bodega, San Carlos)
- Other areas (e.g., San Francisco Peninsula) also with significantly high endemism



Stebbins & Major (1965) *Ecol Monogr*

Range-weighted turnover among significant centers of species endemism





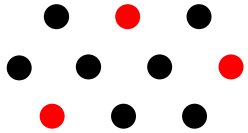
Jepson Bioregions

The Jepson eFlora:

http://ucjeps.berkeley.edu/eflora/

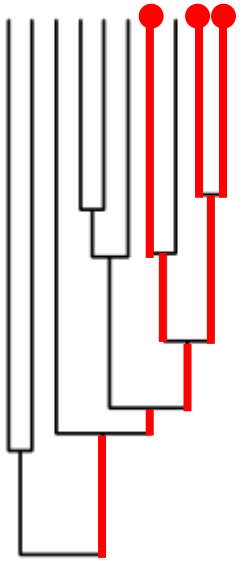
What is biodiversity?

Species richness

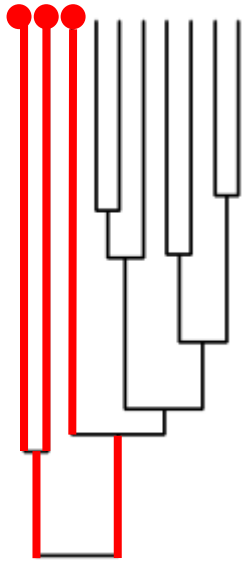


3 species

Phylogenetic diversity

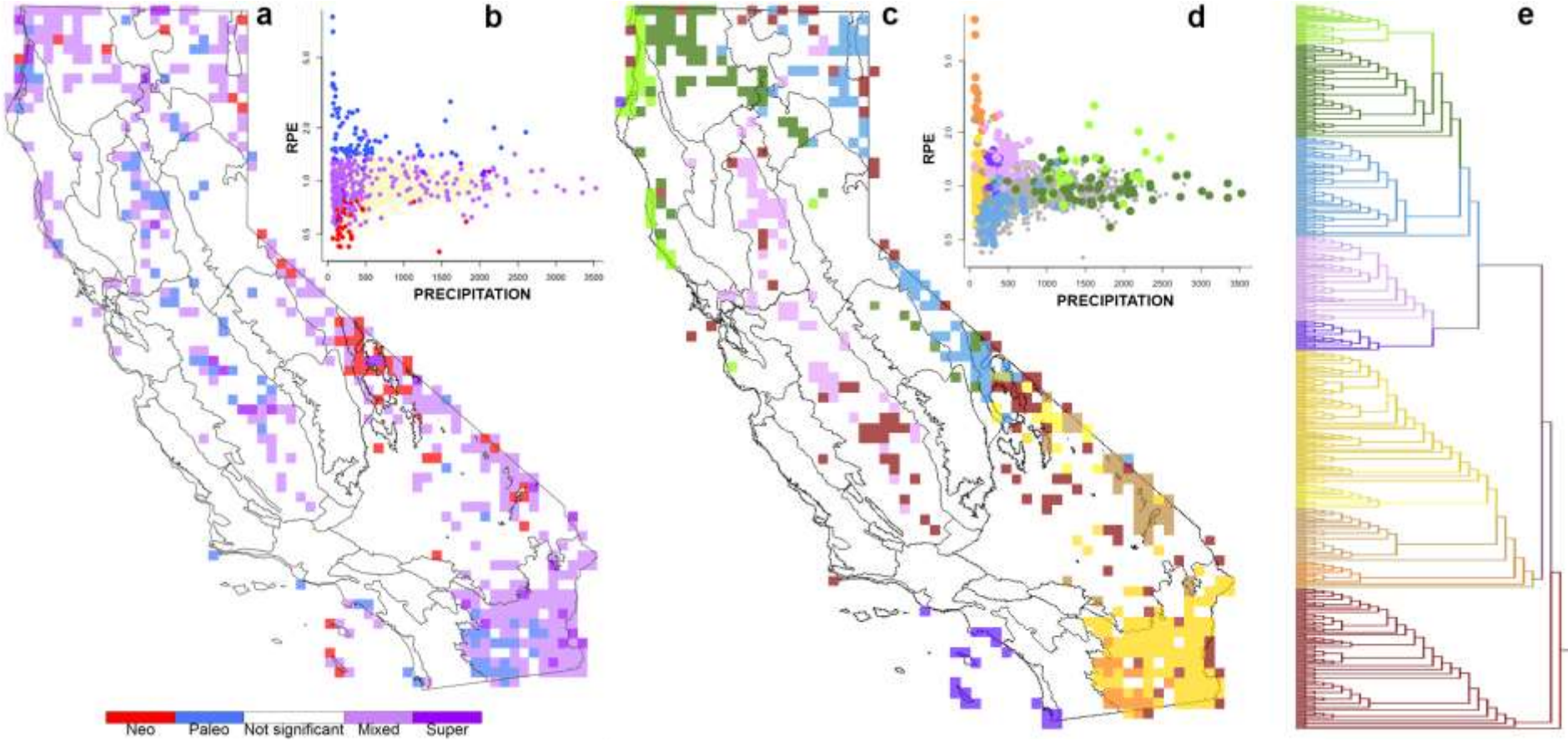


7 My



20 My

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



CANAPE results

Range-weighted phylogenetic turnover among significant centers of endemism detected by CANAPE

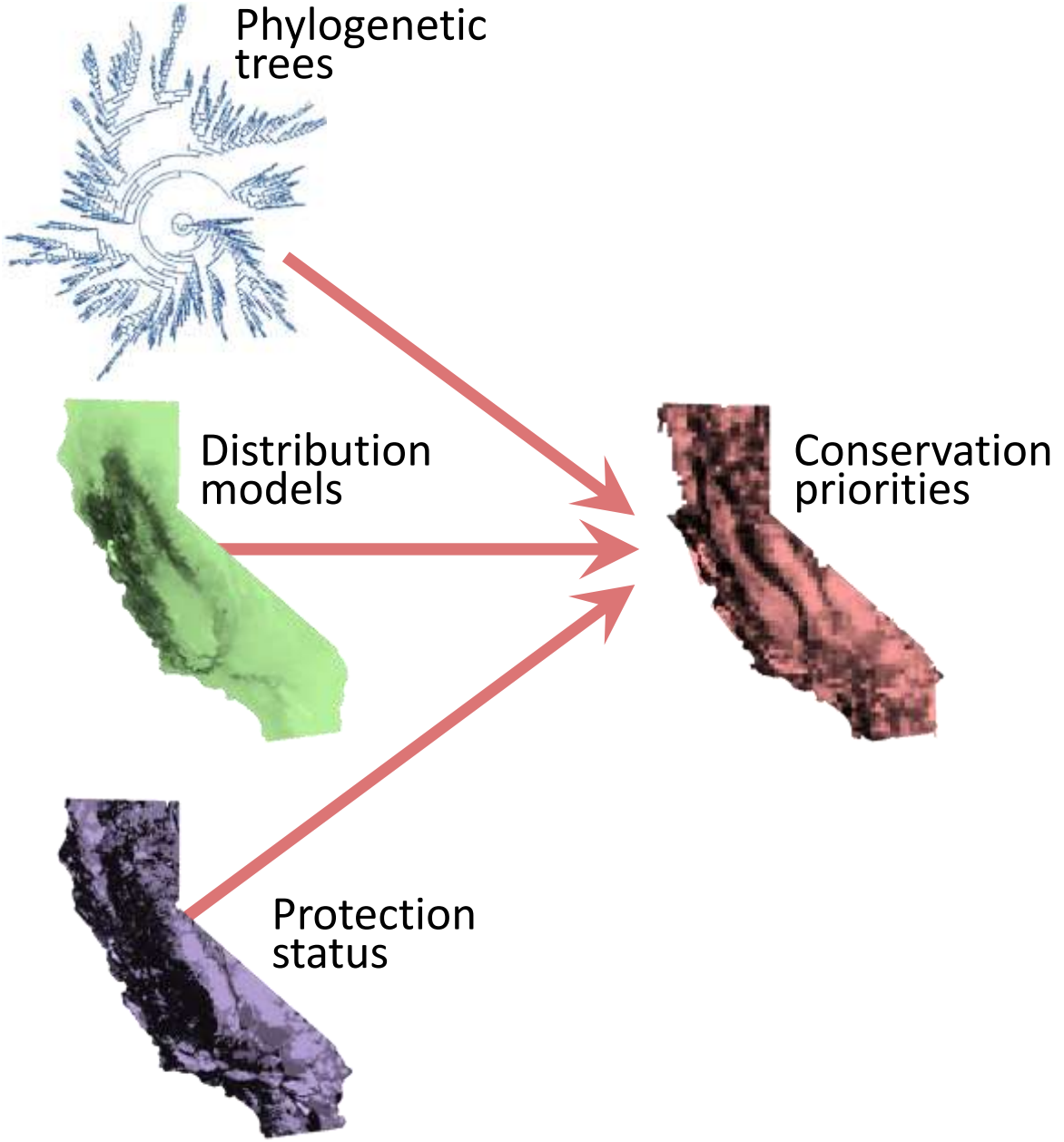
Thornhill et al. (2017) *BMC Biology*

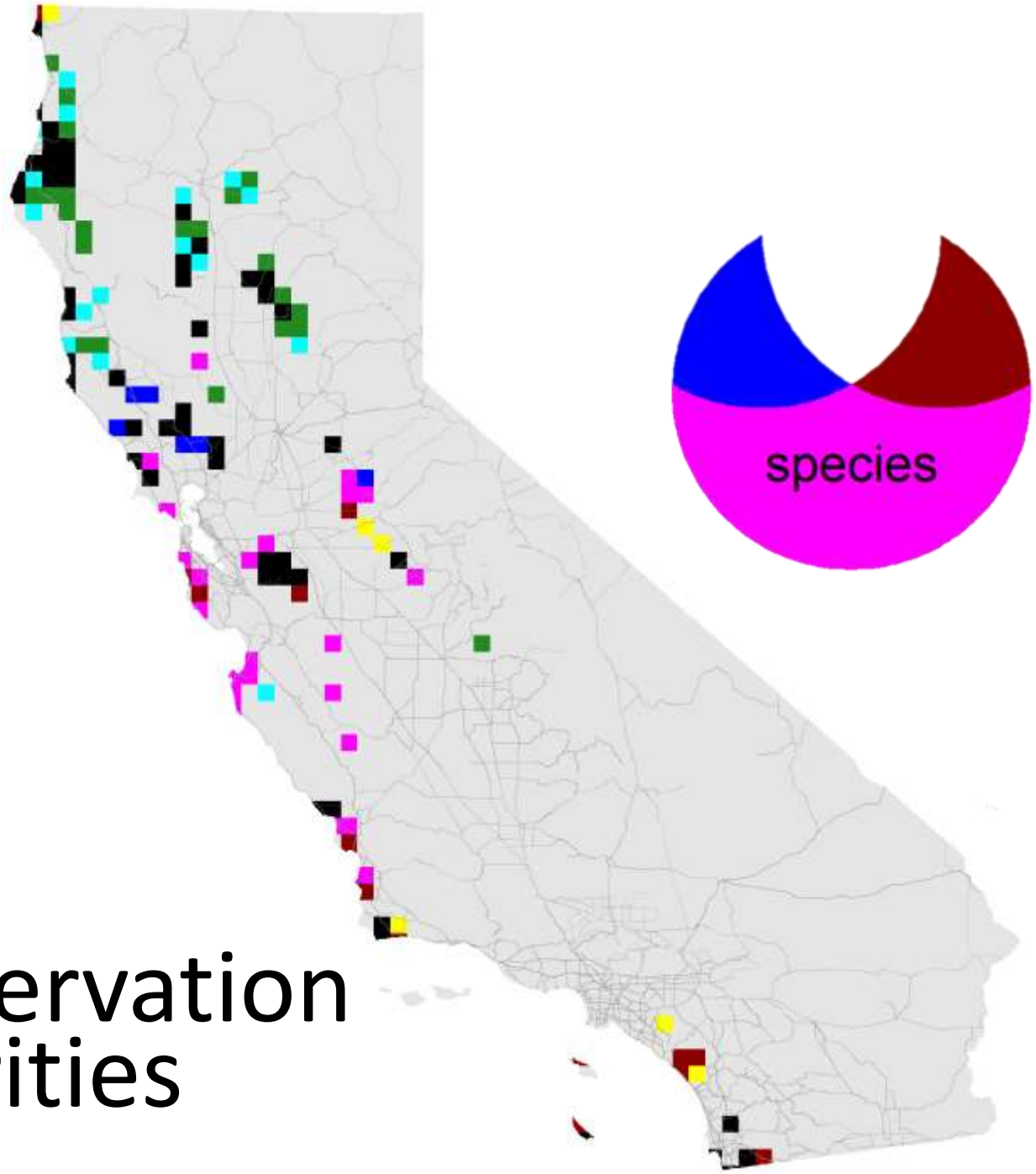
Where are the priority conservation areas based on different biodiversity measures?

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

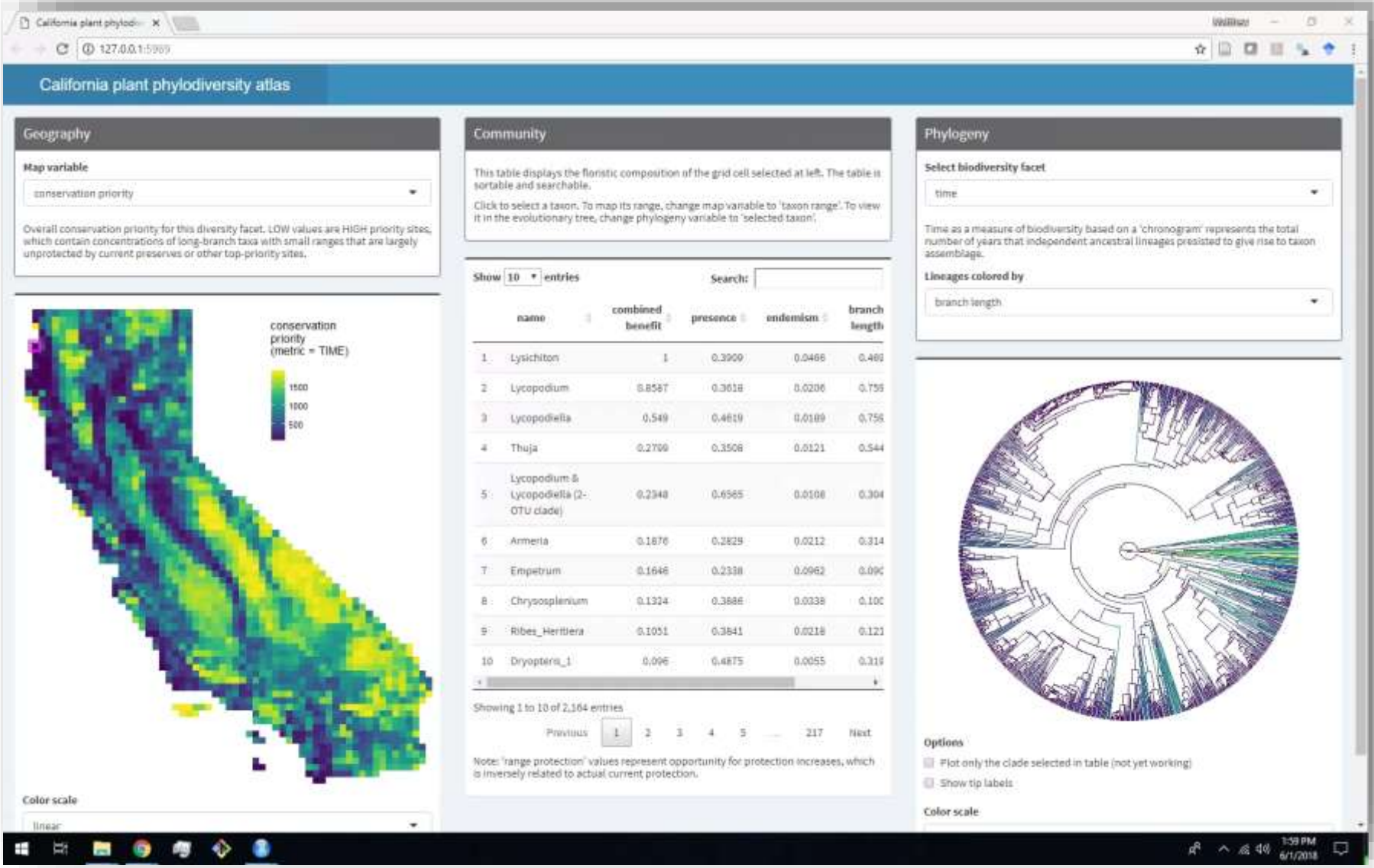
Consensus areas of high conservation priority across different biodiversity facets

Cape Mendocino / Humboldt Bay region

Northern Sierra Nevada foothills

Mt. Hamilton Range

California Plant Phylodiversity Atlas (designed by M. Kling): A new conservation & floristic resource of the CPPP (JEPS)



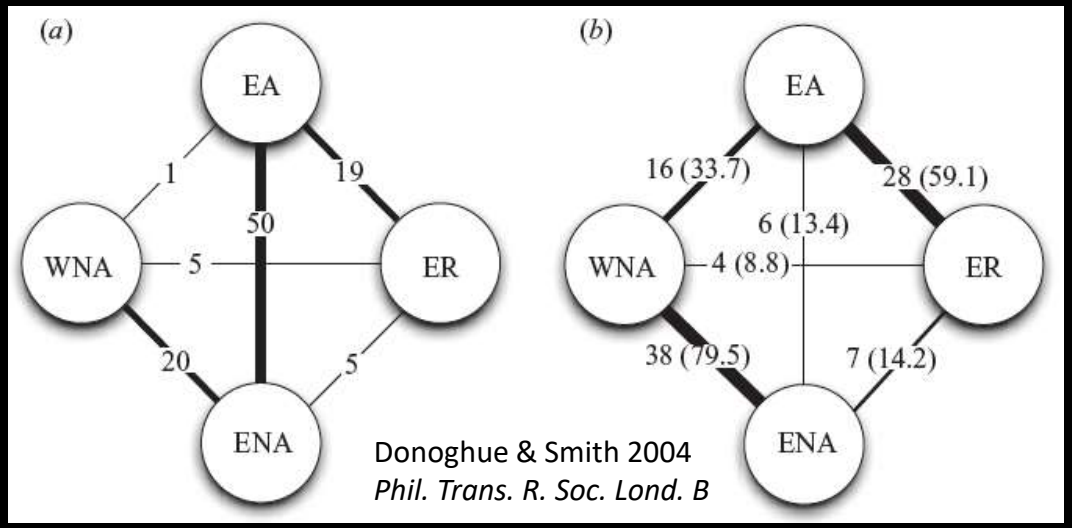
Conclusions about CA flora

- 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

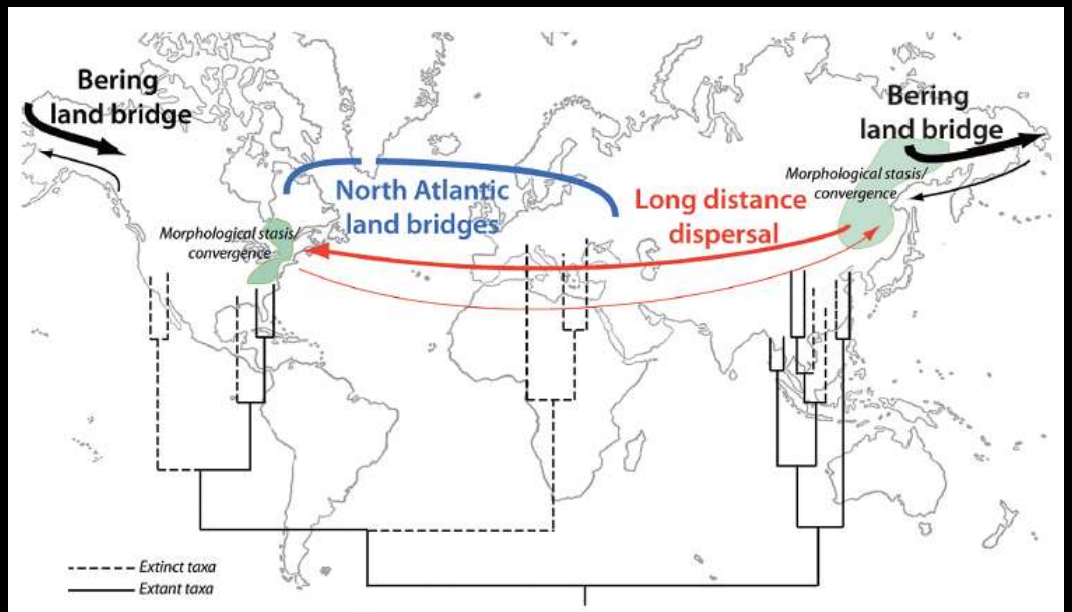
ACKNOWLEDGMENTS

- Lawrence R. Heckard Endowment Fund and National Science Foundation for support
- David Ackerly, Brent Mishler, and many others (especially Jepson staff & students) for assistance

A general finding for Eurasian-North American disjunctions: west. N. Amer. taxa usually most closely related to east. N. Amer. taxa

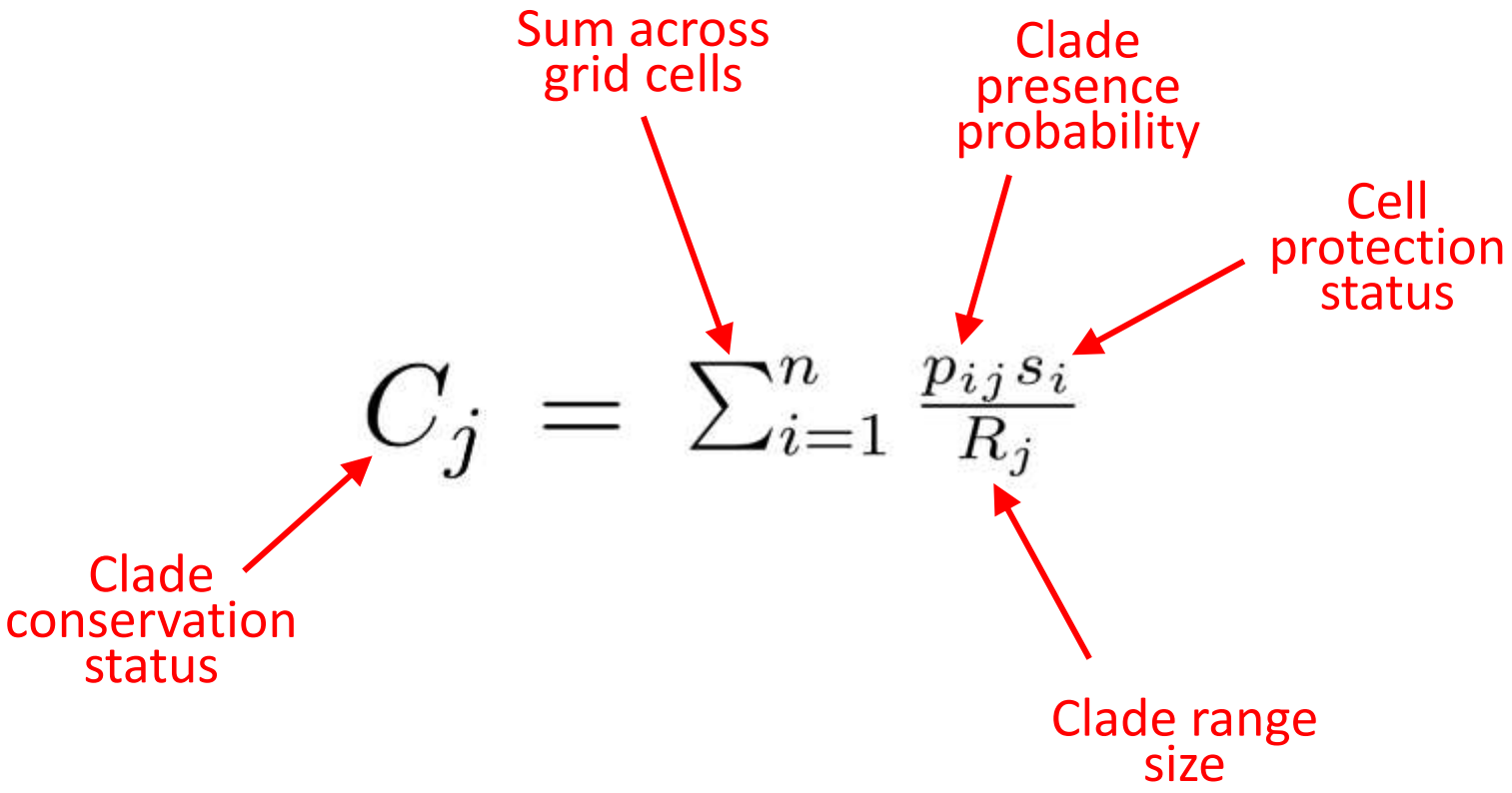


Donoghue & Smith 2004
Phil. Trans. R. Soc. Lond. B



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

▲ Fig. 3
A generalized model of the evolution of the eastern Asian–eastern North American biogeographic disjunctions.

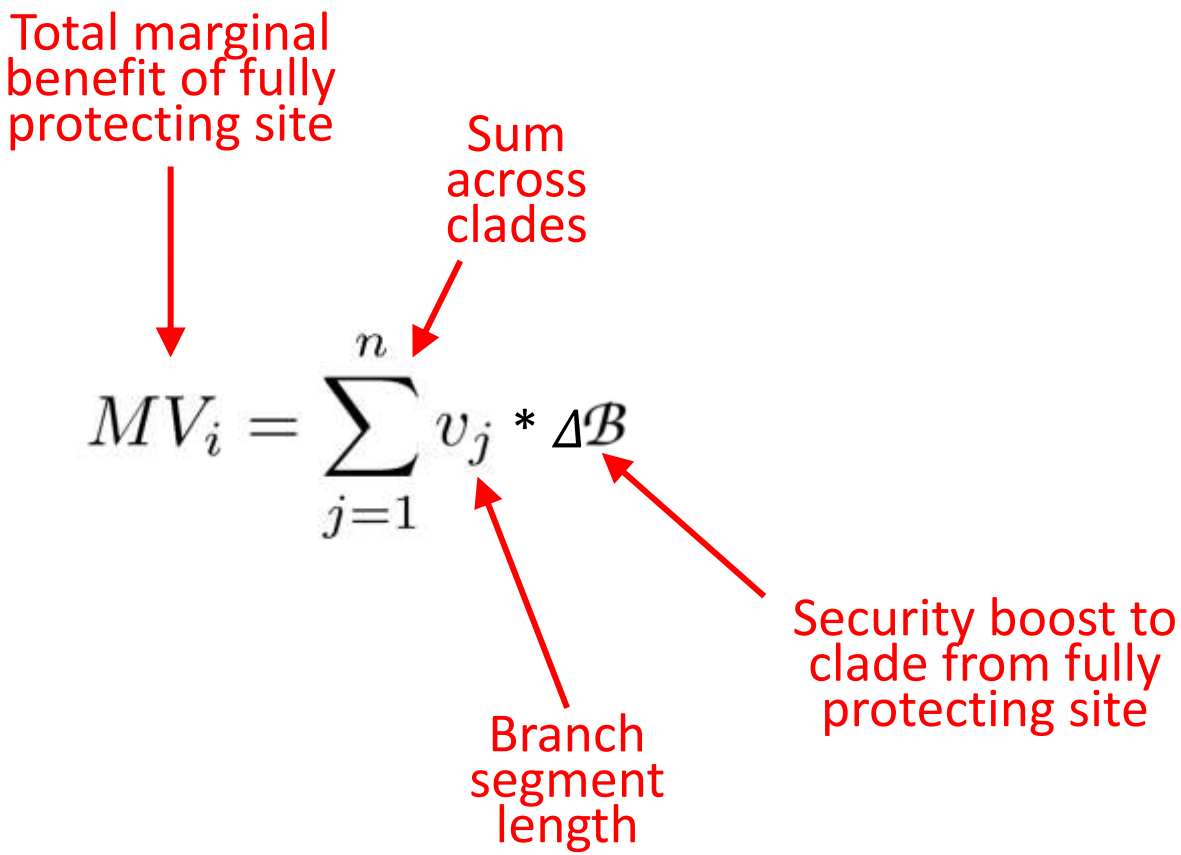

Sum across grid cells
Clade presence probability
Cell protection status
$C_j = \sum_{i=1}^{n} \frac{p_{ij} s_i}{R_j}$
Clade conservation status
Clade range size

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
Sum across clades
$MV_i = \sum_{j=1}^{n} v_j * \Delta\mathcal{B}$
Branch segment length
Security boost to clade from fully protecting site

$$MV_i = \sum_{j=1}^{n} v_j * \Delta\mathcal{B}$$

Stepwise optimization algorithm:

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