$10.00 (free to members)

VOL. 45, NO.3 • November 2017

FREMONTIA

JOURNAL OF THE CALIFORNIA NATIVE PLANT SOCIETY

SPECIAL ISSUE:
Islands of the Californias

California Native Plant Society
2707 K Street, Suite 1
Sacramento, CA 95816-5130

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Lead Authors

Alfonso Aguirre-Muñoz is an oceanographer with an interdisciplinary Ph.D. in Regional Studies and Sustainable Development. He has forty years of professional trajectory in the conservation and sustainable development of coastal, marine and island ecosystems and was the former Director General of GECI (2002 to 2017).

Matt Guilliams is the Tucker Plant Systematist at the Santa Barbara Botanic Garden. A native Californian, Matt has worked with the plants of the state since 1998. At the Garden he focuses on biodiversity of the Central Coast and Channel Islands, as well as on studies of the Boraginaceae and Montiaceae.

Steve Junak has been exploring the California Islands and studying their plants for almost 50 years. He worked as a botanist at the Santa Barbara Botanic Garden for 37 years, has retired from that job, and is currently a Research Associate there. He co-authored the Flora of Santa Cruz Island (1995), wrote the Flora of San Nicolas Island (2008), and is currently working with several other authors on a flora for Catalina Island.

Denise Knapp has a Ph.D. in Ecology from the University of California, Santa Barbara and an M.A. degree in Geography from the University of California, Los Angeles. She has worked on vegetation, fire ecology, invasive species, rare plant, and habitat restoration projects; her current focus is plant-insect interactions, especially pollinators. She has worked as an ecologist in California, particularly the Channel Islands, for two decades.

John Knapp's love-affair with the California Islands started when, at two years old, his father would leave him to play on Tin Can Beach (now Bolsa Chica) while he went for a run, and John would look across the Catalina Channel at the mountain in the sea wondering what awaited him out there. What he found was great beauty and the need for dramatic conservation intervention, and after working on the islands for the past two decades he now serves as the California Islands Ecologist with The Nature Conservancy. His goal is to develop strategies, methodologies, and tools to more effectively and efficiently address the conservation challenges facing the islands, which is best summarized by Willis Linn Jepson who wrote in 1907, "*In the long run protection must come by the devices and resources of united effort, high intelligence, and careful handling.*"

David Merzurkewicz is a Wildlife Biologist for Channel Islands National Park focused on seabirds and habitat restoration. He has been working on the California Islands for the past decade. The scope of his work within the Park encompasses ecological restoration for seabird nesting habitat and associated plant communities as well as spearheading the Park's Inventory and Monitoring program for seabirds.

Kathryn McEachern is interested in exploring how changes in the environment affect populations of rare and endangered plants. She is a Research Plant Ecologist with the U.S. Geological Survey - Western Ecological Research Center's Channel Islands Field Station, in Ventura, California. She has been studying the distribution, abundance and demography of rare plants on the northern Channel Islands for nearly 20 years, providing research to inform and test restoration and recovery actions.

Bryan Munson is the Botany program manager for Naval Base Coronado, which includes San Clemente Island and 7 properties in San Diego County. Bryan has worked in environmental compliance for the Navy for 10 years. Bryan graduated from the University of Wisconsin-Madison with a B.S. in Biology and a minor in Environmental Studies.

Tom Oberbauer has had a lifelong interest in islands and has had the opportunity to visit most of the California and Baja California Pacific Coast Islands as well as many in the Sea of Cortez. He has written a number of articles describing the botany of the islands including for *Fremontia.*

Federico Méndez-Sánchez is an oceanographer with a MSc in Environmental Management from The University of Auckland, New Zealand. He also has twelve years of experience working on conservation, restoration, and sustainable development of the islands and has been the Director General of GECI since March 2017.

John Randall is a Lead Scientist for The Nature Conservancy's California Chapter. He supervises a team of four other scientists working to conserve and manage protected areas and corridors with the aim of linking them into a statewide network. His own work is currently focused on the conservation and management of the biodiversity of the Islands of the Californias, and on contributing to an urban conservation program for Greater Los Angeles by assessing the distribution of biodiversity and opportunities for enhancing it across the region.

THE REMARKABLE FLORA OF THE CALIFORNIA ISLANDS

C. Matt Guilliams[1], Benjamin Carter[2], Martha Lizeth Taceña-Sánchez[3], José Delgadillo[4], Barbara Holzman[5], Steve Junak[1], Denise Knapp[1], Luciana Luna-Mendoza[6], and Sula Vanderplank[7]

Island systems have long been celebrated as remarkable natural laboratories. By studying the biota of island systems, Charles Darwin and Alfred Russel Wallace independently arrived at the theory of natural selection as the mechanism of evolution. It is no coincidence that these pioneering biologists each had this breakthrough while studying islands, as several island characteristics make them well-suited to showcase nature's evolutionary handiwork. Perhaps most importantly, islands are often small land masses with clear natural boundaries. They may be near continents, as is the case with our California Islands, or truly remote, as in the case of the Hawaiian archipelago. These characteristics, particularly island size and distance to the mainland, were explored in foundational work by MacArthur and Wilson (1967), who articulated mathematical relationships between island size, distance from the mainland, and number of species expected on an island. They found that smaller islands situated farther from the mainland support, on average, fewer species than larger and closer islands. As discrete land masses with relatively few species, islands may be less ecologically complex than continental settings at similar latitudes. Ultimately, these relationships may make it easier for scientists to untangle the "story" of how island communities formed through time and how constituent species evolved.

For islands never connected to the mainland, the story of its flora begins with the voyage of a single seed, spore, or structure capable of generating a new plant. What is the long-term fate of a potential colonist after making this voyage across the ocean? Certainly most propagules fail to establish new populations and, of those that do survive, most will establish popula-

Above: A view across the Torrey pine (*Pinus torreyana*) grove on Santa Rosa Island with Santa Cruz Island in the distance. Photograph by Rick Halsey.

1. Santa Barbara Botanic Garden
2. San José State University
3. Centro de Investigaciones Biológicas del Noroeste
4. Universidad Autónoma de Baja California
5. San Francisco State University
6. Grupo de Ecología y Conservación de Islas
7. Centro de Investigación Científica y de Educación Superior de Ensenada

PALEO- AND NEO-ENDEMISM ON THE ISLANDS

PALEO-ENDEMISM

Left: Miocene age fossil leaf of *Lyonothamnus parvifolius* (Axelrod) Wolfe from Stewart Valley, NV (UCMP 38654). Photograph by Diane Erwin. Right: Showy inflorescence of the paleo-endemic genus *Lyonothamnus*, island ironwood (*Lyonothamnus floribundus* subsp. *aspleniifolius* shown here). Photograph by Steve Junak.

NEO-ENDEMISM

Clockwise from top left: Examples of neo-endemism on the California Islands include *Cistanthe guadalupensis*, endemic to Guadalupe Island (Photograph by Jon Rebman). *Eriogonum grande* subsp. *timorum* is endemic to San Nicolas Island. *Galium catalinense* subsp. *acrispum*, is endemic to San Clemente Island. *Malacothrix junakii* is endemic to Middle Anacapa Island. Last three photographs by Steve Junak.

tions that continue to resemble their close relatives on the mainland. In the case of our near-shore California Island flora, the majority of species differ in minute ways or are morphologically identical to mainland conspecifics. However, many island systems support species that are remarkably different from mainland relatives, and islands are cherished in part for these special plants and the evolutionary stories they tell.

EVOLUTIONARY PATTERNS: ENDEMISM AND DIVERSIFICATION

The study of insular floras has revealed a number of intriguing evolutionary patterns. Perhaps the most notable commonality among many island systems is endemism. An organism is said to be endemic when it occurs in one region, for example an island or island archipelago, and nowhere else. Evolutionary biologists have found it useful to differentiate between two types of endemism that result from different historical scenarios. Paleo-endemic species are narrowly distributed organisms in the present day that were formerly widespread when historical conditions permitted. With a mild climate buffered by the moderating influence of the ocean, island systems may provide ideal conditions for the persistence of paleo-endemic plant lineages. A textbook example for the California Islands is island ironwood (*Lyonothamnus floribundus*). The fossil record shows that the genus *Lyonothamnus* was formerly distributed across the southwestern United States in the early Miocene (ca. 16.1 million years ago). With broad changes in climate since the Miocene, the ironwood is presently restricted to portions of the Channel Islands where suitable climate conditions persist. Not surprisingly, paleo-endemic taxa tend to be relatively old lineages; in the remarkable case of the ironwood, a recent study suggests that the lineage giving rise to *Lyonothamnus* diverged from its common ancestor with other extant Rosaceae in the Cretaceous, between 83 and 92 million years ago (Chin et al. 2014).

Islands may also promote the evolution of neo-endemic species, defined as those that occupy in a relatively small region and have historically never been widespread. The physical boundaries around islands can be a formidable barrier to the exchange of genetic material. Over time, island populations may diverge from those on the mainland, either through natural selection in novel insular environments or through the slow accumulation of new genetic mutations. In contrast to paleo-endemics, neo-endemics are recently diverged from their common ancestors with other species, and are therefore often "young" in a geologic sense. Discussed in greater detail in the sections that follow, the California Islands are home to many neo-endemic species.

The Guadalupe Island neo-endemic tarweeds (*Deinandra frutescens, D. greeneana* subsp. *greeneana*, and *D. palmeri*) arose since the late Pliocene, well after the origin of Guadalupe Island and diversification of annual, mainland Californian lineages of *Deinandra* (Baldwin 2007). Top: *Deinandra frutescens* photograph by Reid Moran. Middle: *Deinandra palmeri* photograph by Jon Rebman. Bottom: *Deinandra palmeri* photograph by Steve Junak.

The colonization of an island or island system may result in a burst of diversification resulting in the formation of a group of closely related, neo-endemic taxa. Increased rates of biological diversification yielding a number of species over a short period of time is called a radiation. When these species diversify into novel ecological settings, this burst of diversification is often called an adaptive radiation, one of nature's most celebrated phenomena. The shrubby tarweeds (*Deinandra;* Asteraceae) provide the most thoroughly studied example of adaptive radiation across the California Islands, displaying both recent diversification (within the last 1.9 +- 0.6 million years) and ecological differentiation on Guadalupe Island (Baldwin 2007).

The California Islands are also home to a number of species radiations that may or may not include adaptation to novel ecological settings. Our native western North American *Malva* taxa (Malvaceae) provide an excellent example of diversification across the California Islands, with 5-6 recognized taxa scattered from the northern Channel Islands to Asunción Island off the coast of Baja California Sur, Mexico. These plants differ in a number of features including overall stature, leaf shape and pubescence, and petal color, size, and margin. Evolutionary biologists have also presented strong evidence for the radiation of two groups of trefoils—*Acmispon argophyllus* (Fabaceae; threeisland taxa) and *A. dendroideus* (a separate colonization and diversification comprising three island taxa) as well as two groups in the buckwheats—the *Eriogonum grande* group (Polygonaceae; four island taxa) and the *E. giganteum - E. arborescens* group (a separate colonization and diversification comprising four taxa). Further phylogenetic study will likely reveal insular diversifications in the live-forevers (*Dudleya,* Crassulaceae; 14 island-endemic taxa), island malacothrix (*Malacothrix,* Asteraceae; nine island-endemic taxa), and the bedstraws (*Galium,* Rubiaceae; eight island-endemic taxa).

PHYSICAL FEATURES OF ISLAND PLANTS

The physical features of island plants are often different from their closest relatives on the mainland. One recurring pattern is secondary or insular woodiness, first noted by Darwin (1859) and greatly elaborated upon by Carlquist (1965). Island plants are said to be secondarily woody when it can be demonstrated that they evolved from an herbaceous ancestor. Secondary woodiness is thought to be favored in island settings for a variety of reasons, including a mild, stable climate and the absence of large herbivores. Excellent examples of secondary woodiness can be seen in Guadalupe Island rock daisy (*Perityle incana,* Asteraceae) and in the shrubby tarweeds mentioned earlier. Prolonged growth and woodiness may lead to insular gigantism, a phenomenon aptly displayed by the spectacular Santa Catalina Island buckwheat (*Eriogonum giganteum* var.

Malva lindsayi is endemic to Guadalupe Island. Photograph by Reid Moran.

giganteum, Polygonaceae), which can grow to a staggering 12 feet tall.

In the absence of browsing pressure from large herbivores, island plants may lose energetically costly defensive traits such as spines, tough leaves, and chemical deterrents. After comparative study of island-mainland species pairs, Bowen and Van Vuren (1997) found a loss of leaf defensive traits in island Catalina cherry (*Prunus ilicifolia* subsp. *lyonii,* Rosaceae) and northern island bush poppy (*Dendromecon rigida* subsp. *harfordii,* Papaveraceae). An on-going study at UC Davis shows that plants of the genus *Stachys* (Lamiaceae) on the northern Channel Islands have lost much of their chemical defenses when compared to plants of the same species that grow on the mainland (Freedman, personal communication).

THE CALIFORNIA ISLANDS: REGIONAL FLORAS

The California Islands are world-renowned as centers of endemism and as locations that exhibit many of the morphological patterns observed in insular plants. What follows are sections highlighting the floras of three major groups of California Islands.

The Farallon Islands

The Farallon Islands are a small group of rocky islands located approximately 48 km (30 mi) west of San Francisco. The archipelago includes four islands which are part of the 0.85 km^2 (0.33 mi^2) Farallon National Wildlife Refuge managed as a partnership between the US Fish and Wildlife Service and Point Blue Conservation Science. Of granite and quartz diorite parent material, the islands are conspicuously rocky and uneven, with only minor soil layering in

Left: Maritime goldfields (*Lasthenia maritima*) and gulls on Southeast Farallon Island. Photograph by Quentin Clark.
Right: Close up of *Lasthenia maritima*. Photograph by Barbara Holzman.

the low-lying marine terraces. Due to the harsh environment, the flora of the Farallon Islands includes only 46 plant taxa, only twelve of which are native to California. Of the 34 non-native taxa, twelve are listed as invasive by the California Invasive Plant Council. The most common native plant is the annual maritime goldfields (*Lasthenia maritima,* Asteraceae), a guano specialist occurring on offshore rocks and seabird nesting islands from Central California to Vancouver Island, British Columbia. Other prominent native species include miners' lettuce (*Claytonia perfoliata* subsp. *perfoliata,* Montiaceae) and the stout herbaceous perennial, sticky sand-spurrey (*Spergularia macrotheca* var. *macrotheca,* Caryophyllaceae). Together, maritime goldfields and sticky sand-spurrey constitute a fairly distinct vegetation assemblage on the northwestern marine terrace of Southeast Farallon Island, with dense mats of low-growing sand-spurrey interspersed with maritime goldfields and non-native species. The peak of vegetative growth and flowering coincides with the beginning of the seabird breeding season from March through April, during which time the goldfields are collected by cormorants and gulls for ground nest building material. Later in the summer, dried goldfields are used as hiding cover for gull chicks.

Anthropogenic disturbance is a major issue on the Farallons, with Southeast Farallon Island having a record of human activity dating to 1579 (White 1995). Human impacts include seal hunting, egg collection, plant cultivation, and building construction. Humans have also introduced non-native species like domestic cats (*Felis catus*), European rabbits (*Oryctolagus cuniculus*), and Eurasian house mice (*Mus musculus*). Recent eradication efforts successfully eliminated cats and rabbits (USFWS 2009). Today, introduced plant species outnumber native species 3:1, with the most prominent being New Zealand spinach (*Tetragonia tetragonoides,* Aizoaceae), which forms extensive mats, reducing species richness and hindering seabird burrowing and nesting efforts. Major efforts are underway to eliminate *Tetragonia* and restore native habitat.

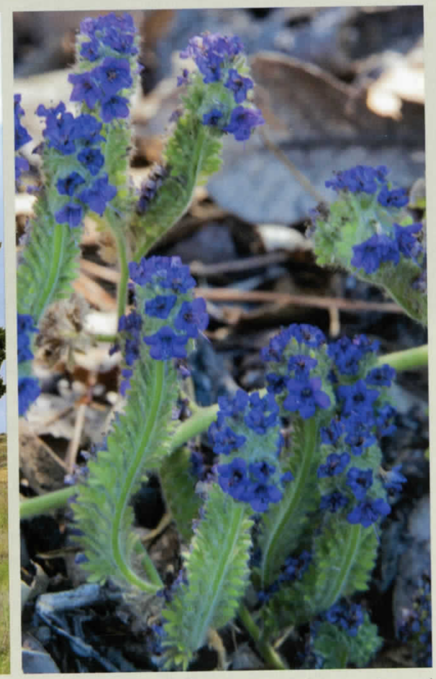
The California Channel Islands

The eight Channel Islands are situated off the coast of southern California between Santa Barbara and San Diego. The islands are described as having two subgroups: the near-shore northern Channel Islands of San Miguel, Santa Rosa, Santa Cruz, and Anacapa, and the more widely-spaced southern Channel Islands of Santa Barbara, San Nicolas, San Clemente, and Santa Catalina. Islands in the archipelago range in size from Santa Cruz Island at 250.0 km^2 (96.5 mi^2) to Santa Barbara Island at 2.6 km^2 (1.0 mi^2) and distance to the mainland ranges from 19 km (12 mi) to 99 km (62 mi). Although none have been connected to the mainland, evidence suggests that the northern islands were historically connected to each other during the early Holocene (ca. 9,000 thousand years ago) when global sea levels were lower.

The flora of the Channel Islands is well studied, owing to a long history of botanical collecting (See Junak, this volume). Nearly all of the islands have been the subjects of detailed floristic and taxonomic work, which recently has included important studies of non-vascular plants (mosses, hornworts, and liverworts; Carter 2015) and lichens. Taxon richness across the islands ranges from 150 natives on Santa Barbara Island to 662 natives on Santa Cruz Island, corresponding well to predictions based on island size. The most common families across the islands are Asteraceae (162 taxa, ~16.5% of the flora), Poaceae

ENDEMIC PLANTS OF THE BAJA CALIFORNIA PACIFIC ISLANDS

The Baja California Pacific Islands are home to a large number of endemic plants. While insular endemics occur on each island or island group, Guadalupe Island is a botanical marvel. It has more island endemic plants than the other seven Baja California Pacific Islands combined. Images below feature Guadalupe Island endemics. Photographs © GECI Archive/J.A. Soriano.



From left to right: Guadalupe Palm (*Brahea edulis,* Arecaceae), Guadalupe cypress (*Hesperocyparis guadalupensis,* Cupressaceae), and Guadalupe Island phacelia (*Phacelia phyllomanica,* Hydrophyllaceae).

(97 taxa, ~10% of the flora), Fabaceae (78 taxa, ~8% of the flora), and Brassicaceae (41 taxa, ~4% of the flora).

Mirroring patterns seen in island systems across the world, the Channel Islands are rich in endemic species, with the 98 insular endemic taxa representing a precious but threatened part of our natural heritage. These taxa have been historically imperiled by the human introduction of invasive animals. Since most non-native animals have been removed, some of the insular endemic taxa are now recovering (see Munson et al. this issue). Other taxa have not been observed since the time of the early collectors such as *Diplacus traskiae* and *Lycium verrucosum*, and are now the targets of rediscovery programs.

The Baja California Pacific Islands

The Baja California Pacific Islands comprise eight islands or island groups. Seven of these are near-shore continental islands, while Guadalupe is a true oceanic island approximately 260 km (161 mi) offshore. Guadalupe Island is part of the Guadalupe Island Biosphere Reserve, Natividad Island belongs to the El Vizcaíno Biosphere Reserve and the other six islands or island groups are included in the Pacific Islands of the Baja California Peninsula Biosphere Reserve (see Aguirre-Muñoz and Méndez-Sánchez this issue). All islands are managed by the Natural Protected Areas Commision (CONANP), the Mexican Navy (SEMAR), the Ministry of Interior (SEGOB) and the Ministry of Environment (SEMARNAT).

The islands range in size from San Jerónimo, at just 0.5 km^2 (0.2 mi^2) and home to seven native plants, to Cedros which is the largest of all the California Islands at 350 km^2 (135 mi^2) in area and with 276 native plants. The vegetation of the northernmost islands is dominated by maritime succulent scrub and species typical of the California Floristic Province, which slowly gives way to an increasing number of arid-adapted species south through the archipelago. The larger islands exhibit this same gradient from their northern to southern extremes, and the southernmost island (Natividad) is dominated by cacti and arid-adapted species. All but two of the Baja California Islands are home to single island endemic plants and all eight are home to specialized insular plants that are endemic to multiple islands.

Of the near-shore islands, it is unsurprising that the largest (Cedros) has the greatest number of endemic plants, while the smaller island complexes of the San Benito Islands (3.9 km^2; 1.5 mi^2) and the Coronado Islands (1.7 km^2; 0.6 mi^2) have three endemic plants each (Vanderplank et al. 2017). The oceanic Guadalupe Island is quite unique, with almost one-third of its native flora being found nowhere else on earth. It has more endemic plants than the other seven islands combined and the known flora includes at least 176 native plants. Researchers continue to discover plants that were presumed extinct, plants that are new records for Guadalupe Island, and some that are new to science.

The removal of non-native herbivores from the islands has been key to the survival of many endemic island plants, particularly on the near-shore islands, but Guadalupe Island suffered several plant extinctions prior to the eradication of the goats. Of the 34 taxa endemic to the island, 3 are now considered extinct, including the paleo-endemic *Hesperelaea palmeri* (Oleaceae), *Castilleja guadalupensis* (Orobanchaceae), and *Pogogyne tenuiflora* (Lamiaceae). When considering the entire flora of the island, 26 native species have been lost. The population of California juniper (*Juniperus californica,* Cupressaceae) is on the way to extirpation with fewer than ten individuals, all in poor condition. This species and many others are the focus of ongoing restoration projects.

THE FUTURE OF CALIFORNIA ISLAND BOTANY

We are currently in a critical time for plant science and conservation on the California Islands. Prudent conservation decisions such as removing non-native herbivores have resulted in vegetation and species recovery, however not all communities and individual taxa have recovered to the same extent. It is clear that there is more to learn about these biological systems and more conservation work yet to be done. Scientists and conservationists have important roles to play in the coming years.

Effective conservation planning relies upon the availability of high quality scientific data. This means it is critical to focus on understanding biological diversity across the archipelago and across taxonomic groups. While the vascular plant flora of the Farallon and Channel islands has been relatively well-studied, the California Islands continue to yield new discoveries. Timely improvements in our knowledge of marine algae, bryophytes, lichens, and biological soil crusts have occurred in the last decade. Of course, these organisms do not exist in isolation—each is connected to others in a complicated ecological network. As a result, conservation of a target species may involve studying its ecological relationships and taking action to preserve an important pollinator or to reduce the effect of a seed predator.

Plant science across the archipelago will continue to benefit from new technologies and innovative study approaches. Genetic techniques are now routinely applied to questions ranging from the distribution of genetic variation on the landscape within a species to understanding the evolutionary history of entire floras. Distribution modeling can be used to predict the occurrence of rare species, sometimes with impressive accuracy. These new tools are needed now more than ever, as we continue our stewardship of the remarkable flora of the California Islands.

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C. Matt Guilliams: mguilliams@sbbg.org