New and Noteworthy Epiphytic Ferns from the Urban Forests of Coastal Southern California, U.S.A.

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ABSTRACT

Davallia solida (G. Forst.) Sw. (Davalliaceae), *Phlebodium aureum* (L.) J. Sm. (Polypodiaceae), *Phlebodium pseudoaureum* (Cav.) Lellinger (Polypodiaceae), and *Rumohra adiantiformis* (G. Forst.) Ching (Dryopteridaceae) are epiphytic ferns native to the subtropical and tropical regions primarily of the Southern Hemisphere. These cultivated ornamental ferns are reported here for the first time growing without direct human assistance in the urban forests of coastal southern California. *Sphaeropteris cooperi* (Hook. ex Muell.) R.M. Tryon (Cyatheaceae), a popular ornamental tree fern native to the subtropical rainforests of eastern Australia, has naturalized on the rocky cliffs of Santa Catalina Island, southern California. We report the first documented mainland occurrences of this species growing as an epiphyte in coastal urban southern California. The known epiphytic occurrences documented for *Nephrolepis cordifolia* (L.) C. Presl (Nephrolepidaceae) and *Psilotum nudum* (L.) P. Beauv. (Psilotaceae) for the urban forests are also provided. Apparently for the first time in California or elsewhere, we report the known epiphytic occurrences of *Cyrtomium falcatum* (L.f.) C. Presl (Dryopteridaceae). Our findings suggest the southern California coastal urban forest environment promotes the dispersal and establishment of non-native epiphytes by facilitating interactions between cultivated phorophytes and several epiphytic ferns escaping cultivation. The ferns have been introduced by horticulture and escaped from gardens, events that represent an important colonization pathway for the invasion of southern California's urban forests. We hope that our findings will stimulate discourse and motivate others to study further the epiphytic ferns of California and other Mediterranean climate regions around the world.
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KEY WORDS: *Cyrtomium falcatum*, *Davallia solida*, *Nephrolepis cordifolia*, *Phlebodium aureum*, *Phlebodium pseudoaureum*, *Psilotum nudum*, *Rumohra adiantiformis*, *Sphaeropteris cooperi*, biological invasions, California, epiphytes, ornamental horticulture, *Phoenix canariensis*, urban forests.

The identity, frequency, and distribution of the non-native plants growing spontaneously outside of cultivation in California have historically been under-reported, even ignored (Hrusa et al. 2002). Also, the non-native plants are frequently given low priority by collectors, which has contributed to gaps in our knowledge (Baldwin et al. 2012). Because invasions of non-native species can significantly impact biodiversity, ecosystem function, human well-being, agriculture and/or commerce, scientists now pay more attention to new introductions (Mack & Lonsdale 2001; Pyšek et al. 2012; Vilà & Hulme 2017).

California has long been recognized as a hotspot for non-native plant invasions (Bossard et al. 2000). Accordingly, Dean et al. (2008) emphasized the importance of including introduced plants in regional floras, noting that specialized plant communities have also been invaded. Only recently, however, have the non-native epiphytes caught the attention of California botanists (Dean et al. 2008; Ritter 2011; Riefner & Smith 2015; Riefner 2016; CCH 2018) namely *Ficus carica* L., *F. microcarpa* L.f. and *F. rubiginosa* Desf. ex Vent. (Moraceae), *Nephrolepis cordifolia*, and *Psilotum nudum*.

Epiphytes account for approximately 9% of all vascular plant diversity in the world (Nieder et al. 2001; Zotz 2016). Our knowledge of epiphyte communities however, lags far behind that of terrestrial plants, and biogeographical studies are scarce (Kreft et al. 2004; Burns & Zotz 2010). Consequently, the vascular epiphyte diversity and composition for the temperate versus subtropical-tropical climate zones have been poorly documented (Zotz 2005; Hsu & Wolf 2009).

In many temperate regions epiphytes are understudied and little appreciated, but may not be devoid of interesting species (Zotz 2005). Brandes (2007), for example, reported an extensive list of the epiphytes colonizing *Phoenix canariensis* Chabaud (Arecaceae) cultivated in tourist centers around the Mediterranean Sea. Additionally, epiphytes are rarely identified in evaluations for the non-native plant invasions of the world's Mediterranean climate regions nor have they been considered as components contributing to global biotic homogenization (Arianoutsou et al. 2013). Accordingly, little work has been done to document the non-native epiphytic ferns growing spontaneously in coastal southern California.

In this paper, we document occurrences of eight non-native ferns growing epiphytically outside of cultivation in the urban forests of coastal southern California. These ferns grow primarily on the trunks of *Phoenix canariensis*, which is cultivated widely along streets and in parks. Figure 1 depicts a human-planted urban forest in the Mediterranean climate of coastal southern California; it also depicts *P. canariensis* in typical urban settings colonized by the epiphytic ferns.

MATERIALS AND METHODS

We reviewed various classification schemes for the vascular epiphytes and here employ the definition prepared by Zotz (2016). In addition, we describe the urban forest, and outline the field survey program implemented to develop a preliminary conspectus of the non-native epiphytic ferns growing spontaneously in the urban forests of coastal southern California.

Defining Vascular Epiphytes

Vascular epiphytes are "plants that germinate and root non-parasitically on other plants at all stages of life" (Zotz 2016). Many epiphytes, however, grow occasionally on rocks or soil, and conversely many primarily terrestrial plants grow occasionally on living substrates (Zotz 2016). Therefore, this definition resolves most previous problematic classifications for plants that exhibit variable degrees of fidelity to epiphytic life (Zotz 2016).

Zotz (2016) consolidated previous classification schemes into a format that can be readily applied worldwide: 'obligate' epiphytes are species with >95% occurrence of individuals in a particular region growing epiphytically; 'accidental' epiphytes include species with >95% occurrence of individuals growing terrestrially in a region; and 'facultative' epiphytes are those species demonstrating a frequency of occurrence between these two categories, i.e., individuals that are terrestrial and epiphytic. Obligate epiphytes are referable to 'true, typical or holoepiphyte' classifications (Zotz 2016). Therefore, by utilizing a common definition for epiphytic classification scientists can more accurately characterize the structure of epiphytic communities and their biogeographical patterns (Zotz & Bader 2011).

The Urban Forest

An urban area, in a broad sense and adopted here, is defined as a human settlement with high population density and infrastructure of built environment (Wikipedia 2018a). An urban forest is a network comprising all woodlands, groups of trees and individual trees located in urban and peri-urban (transition zone between urban and rural) environments (Salbitano et al. 2016).

America's urban forests comprise over 130 million acres of parks, street trees, landscaped boulevards, gardens, greenways, river, wetland, and coastal promenades, nature preserves, and trees growing at former industrial sites (USDA, USFS 2018). In California, there are an estimated 9.1 million street trees, which comprise about 10–20% of the total urban forest (McPherson et al. 2015). Urban forests provide habitats and services that enrich the quality of life for humans (Jim & Chen 2009). They also provide resources for animals and plants, conserve native biodiversity, and sustain ecological functions in landscapes that are increasingly fragmented by development (Howenstine 1993; Pyšek 1998; Nowak et al. 2010; Rega et al. 2015). Urban environments, however, can be a source of invasive non-native ornamental plants that escape human-planted landscapes (Dehnen-Schmutz et al. 2007).

In southern California, urban forests are diverse, human-planted ecosystems comprising tree species imported from diverse habitats, climates, and continents (Pataki et al. 2013; Avolio et al. 2105). Lesser (1996) reported 257 species in 123 genera for 21 southern California cities. Further, Jenerette et al. (2016) studied the composition of urban forests in 20 cities within the United States and Canada; topping the list for diversity are Los Angeles with 104 tree species, Santa Barbara 85, Irvine 77, and San Francisco with 77. Thus, the urban forests of southern California have been acclaimed as a "Garden of Eden" (Pincetl et al. 2013).

Southern California is also renowned for its iconic and ubiquitous cultivation of palm trees (Farmer 2013; Pataki et al. 2013). Palms are planted frequently along streets and boulevards, parks, business plazas, and in residential communities (Hatch 2007; Avolio et al. 2015); noteworthy are *Washingtonia robusta* H. Wendl., *Washingtonia filifera* (Lindl.) H. Wendl., *Syagrus romanzoffiana* (Cham.) Glassman, *Phoenix canariensis*, *Phoenix dactylifera* L., and *Butia capitata* (Mart.) Becc.

Study Area: Focused Field Survey Program

A survey program to document epiphytic ferns was implemented following the discovery of *Nephrolepis cordifolia* growing on palms in coastal urban southern California (Riefner & Smith 2015). Riefner surveyed coastal Los Angeles, Orange, and San Diego counties from 2014–2018 to document the epiphytic ferns growing spontaneously outside of cultivation in coastal southern California. The surveys focused on public landscapes along streets, boulevards, and freeways, greenbelts around residential housing tracks or business plazas, and county parks and recreation areas.

Wherever epiphytic ferns were located, including palm or non-palm tree hosts, data collection included a physical description of the location, GPS coordinates, notes on the species and population size, host tree species, and photographic documentation. Herbarium specimens were collected, with the exception of sites where ferns were observed growing beyond reach; these ferns were photographed for documentation in lieu of collecting specimens, and the photographs will be posted online.

Scientific names follow the phylogenetic system adopted by the Pteridophyte Phylogeny Group (PPG I 2016). The PPG provides a comprehensive consensus classification by employing a community-based approach following the main tenets of Smith et al. (2006).

RESULTS

No native California ferns were observed. Rather, we documented eight non-native epiphytic fern species in six families originating from a diversity of geographic regions. Table 1 lists the species, nativity, preliminary epiphytic classification, and the host tree(s) recorded during this study.

Table 1. Non-Native Epiphytic Ferns Recorded During the Study for Los Angeles, Orange, and San Diego Counties, Coastal Southern California.

Species	Family	Nativity	Epiphytic Class	Phorophyte(s)
New to California				
Davallia solida	Davalliaceae	Australasia	Obligate	*Phoenix canariensis*
Phlebodium aureum	Polypodiaceae	Subtropical-Tropical Americas	Obligate	*Phoenix canariensis*
Phlebodium pseudoaureum	Polypodiaceae	Subtropical-Tropical Americas	Obligate	*Phoenix canariensis*
Rumohra adiantiformis	Dryopteridaceae	Southern Hemisphere	Obligate	*Phoenix canariensis*, *Butia capitata*
New for the Mainland Coast				
Sphaeropteris cooperi	Cyatheaceae	Eastern Australia	Facultative	*Phoenix canariensis*, *Butia capitata*
Noteworthy Species				
Nephrolepis cordifolia	Nephrolepidaceae	Australasia-Pacific Islands, Neotropics	Facultative	*Phoenix canariensis*, *Butia capitata*, *Washingtonia robusta*, *Pinus pinea*
Psilotum nudum	Psilotaceae	Cosmopolitan: Warm Temperate to Tropical	Facultative	*Syagrus romanzoffiana*, *Phoenix canariensis*
First Documentation of Epiphytic Behavior				
Cyrtomium falcatum	Dryopteridaceae	East Asia	Accidental	*Phoenix canariensis*

Davallia solida, _Phlebodium aureum_, _Phlebodium pseudoaureum_, and _Rumohra adiantiformis_ new to California

Davallia solida, *Phlebodium aureum*, *P. pseudoaureum*, and *Rumohra adiantiformis* have not been previously cited growing spontaneously outside of cultivation in California, including Nauman (1993a), Hrusa et al. (2002), Roberts et al. (2004), Clarke et al. (2007), DiTomaso and Healy (2007), Dean et al. (2008), Roberts (2008), Prigge and Gibson (2012), Smith (2012a,b), Rebman and Simpson (2014), Jepson Flora Project (2018), and the USDA, NRCS (2018). No voucher specimens for *D. solida*, *P. aureum*, *P. pseudoaureum*, or *R. adiantiformis* growing outside of cultivation have been posted for California by the Consortium of California Herbaria (CCH 2018) or the Southwest Environmental Information Network (SEINet 2018).

In addition, *Phlebodium aureum*, *P. pseudoaureum*, and *Rumohra adiantiformis* have not been documented previously growing outside of cultivation along the Pacific Coast of North America. In the United States and its territories, *P. aureum* is native to Florida, Puerto Rico, and the Virgin Islands, and has naturalized in Hawai‘i (Nelson 2000; Vernon & Ranker 2013; Randall 2017; USDA, NRCS 2018). However, there is considerable disagreement regarding its native versus introduced range for Alabama, Georgia, and South Carolina (Snyder & Bruce 1986; Weakley 2015; USDA, NRCS 2018). *Phlebodium pseudoaureum* is native to Puerto Rico, but has not naturalized in Hawai‘i (Lellinger 1985; Imada 2012; Vernon & Ranker 2013; USDA, NRCS 2018). There is also considerable disagreement regarding its nativity or occurrence in Florida (Proctor 1985, 1989; Nauman 1993a; Weakley 2015; USDA, NRCS 2018). *Rumohra adiantiformis* is native to Puerto Rico and has naturalized in Florida, but is not known to occur outside of cultivation elsewhere in the flora region (Lellinger 1985; Vernon & Ranker 2013; Randall 2017; USDA, NRCS 2018).

Voucher specimens (duplicates to be distributed), all from **U.S.A.: CALIFORNIA: _Davallia solida_: Orange Co.:** City of San Clemente, coastal bluff W of West Vista Blanca and S of San Clemente State Beach, 33.39906N -117.60136W, elev. ca. 21 m, rare, epiphytic on trunk of *Phoenix canariensis*, growing with *Asparagus* sp. and *Nephrolepis cordifolia*, 9 Sep 2018, *Riefner 18-115* (UC). **San Diego Co.:** City of Oceanside, along South Freeman St. at Missouri Ave., 33.19235N -117.37518W, elev. ca. 23 m, large clump of rhizomatous plants epiphytic on the trunk of a roadside *Phoenix canariensis*, growing with *Nephrolepis cordifolia*, 30 Sep 2016, *Riefner 16-385* (UC). **_Phlebodium aureum_: Los Angeles Co.:** City of Malibu, Eastern Malibu, W of Carbon Canyon Rd., N side Pacific Coast Highway at Carbon Mesa Rd., 34.03905N -118.65394W, elev. ca. 31 m, epiphytic near ground level to ca. 3 m off the ground, well-established on the trunk of *Phoenix canariensis*, urban landscape, rhizomes intertwined within dense growth of *Ficus rubiginosa* and *Nephrolepis cordifolia*, irrigation spray drift present, 13 Dec 2015, *Riefner 15-469* (UC). **_Phlebodium pseudoaureum_: Orange Co.:** City of Laguna Beach, Aliso Beach Park, W of Coast Highway, 33.50984N -117.75135W, elev. ca. 4 m, rare, epiphytic on trunk of *Phoenix canariensis* cultivated along roadside in urban greenbelt, growing with *Cyrtomium falcatum*, 18 Aug 2018, *Riefner 18-110* (UC). **_Rumohra adiantiformis_: Los Angeles Co.:** City of Venice, along Venice Blvd. between Lyceum Ave. and Walgrove Ave., 33.99804N -118.443365W, elev. ca. 11 m, rare epiphyte on the trunk of *Phoenix canariensis,* urban landscape, irrigation spray present, growing with *Cyrtomium falcatum, Nephrolepis cordifolia*, *Sphaeropteris cooperi,* and *Ficus carica*, 24 Sep 2016, *Riefner 16-375* (UC); City of Long Beach, Belmont Park, Alamitos Bay, Bay Shore Ave. along Appian Way, 33.76007N -118.123531W, elev. ca. 3 m, local, epiphytic on trunk of cultivated *Butia capitata*, growing with *Nephrolepis cordifolia*, urban landscape, 10 Jun 2018, *Riefner 18-64* (UC). **Orange Co.:** City of San Clemente, Cyprus Shore, coastal bluff W of Calle Ariana and S of San Clemente State Beach, 33.39602N -117.59955W, elev. ca. 12 m, abundant epiphytic on trunk of *Phoenix canariensis* cultivated in greenbelt, irrigation spray drift present, growing with *Asparagus* sp., 9 Sep 2018, *Riefner 18-118* (UC). **San Diego Co.:** City of Carlsbad, N of Batiquitos Lagoon, along Batiquitos Dr. at Gabbiano Ln., 33.09822N -117.30276W, elev. ca. 26 m, epiphyte on the trunk of *Phoenix canariensis,* urban landscape, irrigation spray present, 1 Feb 2017, *Riefner 17-52* (UC); City of

Carlsbad, N side of Agua Hedionda Lagoon, along Adams St. E of Highland Dr., 33.14519N -117.32581W, elev. ca. 15 m, locally abundant, epiphyte on trunks of cultivated *Phoenix canariensis* street trees, growing with *Nephrolepis cordifolia*, 30 Jun 2017, *Riefner 17-322* (UC).

***Davallia solida* (Davalliaceae):** *Davallia sensu lato* is widely distributed from the Atlantic Islands to Africa, southern Asia to Malaysia, Polynesia, Australia, New Zealand, and the Pacific Islands (Nooteboom 1994; Yuyen & Boonkerd 2002; Xing et al. 2013). *Davallia* species are small to medium-sized ferns that in the wild are usually epiphytic. Most species are easily recognized by their long-creeping and densely scaly rhizomes, short phyllopodia, finely dissected or pinnatifid blades, and cup-shaped indusia and sori that are nearly marginal on pinnae (Hoshizaki & Moran 2001). Many of the thin-textured davallias are drought-sensitive (Hoshizaki & Moran 2001). *Davallia solida*, however, is drought-tolerant and sheds fronds or parts of the blade during dry seasons (Yuyen & Boonkerd 2002).

A leathery evergreen perennial, *D. solida* is an epiphyte, but occasionally may be epilithic (growing on rocks) or terrestrial. It is widespread in China, Cambodia, Thailand, India, Indonesia, Malaysia, Myanmar, Australia, Papua New Guinea, Philippines, Sri Lanka, Thailand, Vietnam, and the Pacific Islands (Xing et al. 2013; ABRS 2018). Generally, *D. solida* is easily recognized by its dark rhizome, rhizome scales that are ovate-lanceolate with a long subulate apex and ciliate margins, leathery lamina, and tubular indusia (Nooteboom 1994; Xing et al. 2013).

Davallia solida grows in exposed places or in deep shade, including open rocky habitats and savannas or in rainforests from sea level to about 1,500 m (Nooteboom 1994; Xing et al. 2013). In some regions, *D. solida* has been identified as a microhabitat specialist, growing almost exclusively on mangroves (Nakamura 2000; Hayasaka et al. 2012). *Davallia solida* also grows in human-modified habitats, including rubber agro-forest plantations, urban green spaces in Indonesia, and an urban nature preserve in Singapore (Wee 1995; Beukema et al. 2007; Ulfa et al. 2013).

Widely cultivated as an ornamental (Hoshizaki & Moran 2001), including in Hawai‘i (Imada et al. 2018), *D. solida* apparently is not commonly available in the California retail market (Perry 2010; Brenzel 2012). *Davallia solida* is also grown in Florida, Costa Rica, and Africa for commercial production of cut-fronds used by florists (McConnell et al. 1989; Stamps 2017).

Davallia solida is not known to escape cultivation in the United States and its territories (Randall 2017; USDA, NRCS 2018), including Hawai‘i (Imada 2012; Vernon & Ranker 2013), nor has it escaped in Europe (Euro+Med PlantBase 2018). The two known locations documented for *D. solida* growing outside of cultivation in southern California are depicted in Figure 2. Its epiphytic habitat on *Phoenix canariensis* and morphological features are shown in Figure 3, Photographs A–C.

***Phlebodium aureum* (Polypodiaceae):** *Phlebodium* (R. Br.) J. Sm. comprises about four species of primarily epiphytic, or less frequently epilithic ferns, that occur in subtropical and tropical environments of the New World (Mickel & Smith 2004). *Phlebodium aureum* (syn., *Polypodium aureum* L.), a fertile tetraploid, is believed to have arisen through allopolyploidy following hybridization between *P. decumanum* (Willd.) J. Sm. and *P. pseudoaureum* (Cav.) Lellinger (Nauman 1993a; Mickel & Smith 2004). *Phlebodium aureum* is similar to *P. pseudoaureum*, but differs in having sori arranged usually in two rows between the costa and pinna margin, and its fronds are more deeply lobed with generally broader segments (Hoshizaki & Moran 2001; Mickel & Smith 2004). Because they are easily confused, Mickel and Smith (2004) reported that collections identified as *P. aureum* in Mexico are *P. pseudoaureum* (Cav.) Lellinger (syn., *P. areolatum* [Humb. & Bonpl. ex Willd.] J. Sm.).

Phlebodium aureum, a deciduous medium to large perennial, is epiphytic on a variety of trees, decaying logs or humus. In the southeastern United States, Lellinger (1985) and Nauman (1993a) noted it

grows frequently among old leaf bases on the trunks of *Sabal palmetto* (Walt.) Lodd. It is also epiphytic in crotches and crevices of other trees, particularly *Quercus virginiana* Mill. (Fagaceae), but rarely is terrestrial growing on calcareous soils, or epilithic on limestone and masonry (Weakley 2015; Wunderlin et al. 2018). Thereby, *P. aureum* occupies a variety of habitats and microclimates, including mesic to hydric hammocks, swamps, coastal strand and beaches, pine flatwoods, ditches, and ruderal sites (Nauman 1993a; Wunderlin et al. 2018).

Phlebodium aureum can also grow in dry sunny locations, but then the fronds are deciduous and seasonally shed during drought (Benzing 1990; Crouch et al. 2011). Phyllopodia (basal portions of petioles, proximal to articulation planes that remain attached to the rhizomes after old fronds abscise) are an adaptation to an epiphytic habitat and seasonal growing conditions. Deciduous fronds expose the phyllopodia that may help with identification of *Phlebodium* species during drought.

Phlebodium aureum is reported as indigenous to Alabama, Florida, Georgia, Mexico, the West Indies, and Central and South America (Nauman 1993a; USDA, NRCS 2018). However, there is considerable disagreement regarding its range and nativity in the southeastern United States (Lellinger 1985; Weakley 2015; Keener et al. 2018). Weakley (2015) also reported the species has been introduced to Beaufort, Jasper, and Charleston counties, South Carolina, via planting of palmettos.

Because *P. aureum* is epiphytic, epilithic or terrestrial, and tolerant of harsh conditions, it has naturalized in many warm-temperate, subtropical, and tropical regions (Randal 2017). *Phlebodium aureum* is a well-known weed in Hawai‘i. It was first documented in 1909 (Wagner 1950; Wilson 1996) and now grows on all of the main islands (Imada 2012). *Phlebodium aureum* is epiphytic in forests and near habitations, but rarely grows on buildings in Hawai‘i (Wilson 1996). Wagner (1950) observed it as a volunteer growing with *Nephrolepis* sp. on *Phoenix canariensis* in a yard near the Bishop Museum.

Phlebodium aureum is commonly cultivated in South Africa and has escaped in the vicinity of Durban, KwaZulu-Natal, and at Port St. Johns in the Eastern Cape (Crouch et al. 2011). *Phlebodium aureum* grows as an epiphyte in brightly lit situations in moist evergreen riverine forests and their margins, occasionally in exposed situations on ledges of buildings, but is found rarely naturalized on soil (Crouch et al. 2011). *Phlebodium aureum* has also naturalized on Mauritius (Lorence 1978) and sparingly in New South Wales and Queensland, Australia (Pellow et al. 2009; ABRS 2018). It is an occasional escape in the Mediterranean region, i.e., Madeira (Euro+Med PlantBase 2018).

Outside of cultivation in southern California, *P. aureum* grows among the leaf bases and crotches on the trunk of *Phoenix canariensis* within the drift spray zone of landscape irrigation facilities. It is closely associated with other epiphytic ferns and the hemiepiphytic species of *Ficus*. The single known location documented for *P. aureum* is depicted in Figure 2. Its epiphytic habitat on *P. canariensis* and distinctive morphological features are depicted in Figure 4, Photographs A–C.

***Phlebodium pseudoaureum* (Polypodiaceae):** *Phlebodium pseudoaureum* is a deciduous medium to large perennial that is epiphytic, epilithic, or terrestrial in numerous tropical forest ecosystems (Mickel & Smith 2004). Widespread in Central and South America, *P. pseudoaureum* is also reported to be native for Florida and Puerto Rico, but not Hawai‘i (Proctor 1989; Davidse et al. 1995; Mickel & Smith 2004; Imada 2012; USDA, NRCS 2018). Because it is similar to and can be confused with *P. aureum* (Nauman 1993a; Mickel & Smith 2004), its occurrence has been disputed for Florida (Lellinger 1985; Proctor 1985, 1989; Nauman 1993a; Weakley 2015; Wunderlin et al. 2018). *Phlebodium pseudoaureum* differs in having sori arranged in a single row between the costa and pinna margin, venation, and stiffer, slightly more leathery blades (Hoshizaki & Moran 2001; Mickel & Smith 2004).

Phlebodium pseudoaureum is not known to escape cultivation in the United States (Randall 2017; USDA, NRCS 2018), including in Hawai‘i (Vernon & Ranker 2013). Also, it has not naturalized in Europe (Euro+Med PlantBase 2018), Australia (ABRS 2018), New Zealand (NZPCN 2018), or South Africa (Crouch et al. 2011); however, wherever *P. aureum* has naturalized herbarium specimens should be reexamined and additional collections may be needed to assess whether *P. pseudoaureum* has been overlooked.

The epiphytic habitat poses novel ecophysiological challenges to growth and survival, which are relevant for ferns that alternate their life cycle between two distinct free-living phases, gametophytes and sporophytes (Watkins & Cardelús 2012). Since epiphytes are often absent in dry habitats, water shortage and tolerance to dehydration is thought to be the primary limiting abiotic factors for establishment and survival (Benzing 1990; Zotz 2016). True desiccation tolerance in the fern sporophyte phase is known, but likely exists in relatively few species, such as the cheilanthoid species that are frequently associated with xeric habitats (Proctor & Pence 2002; Watkins et al. 2007). Watkins et al. (2007), however, demonstrated that desiccation-tolerance in the gametophytic phase may explain how some ferns have successfully colonized drought-prone habitats, including gametophytes of tropical species such as *P. pseudoaureum*. Gametophytes vary considerably in water content throughout the day, or season, and must be able to withstand long periods of desiccation, especially epiphytic taxa (Watkins 2006). In addition to shedding fronds during drought, *P. pseudoaureum* exhibits other physiological characteristics that may explain how it can colonize an epiphytic habitat in the California arid Mediterranean climate.

Outside of cultivation in southern California, *P. pseudoaureum* grows among the leaf bases and feeder roots on *Phoenix canariensis*, within the drift spray zone of landscape irrigation facilities. The single location documented for *P. pseudoaureum* is depicted in Figure 2. Its epiphytic habitat on *P. canariensis* and distinctive morphological features are shown in Figure 4, Photographs D–F.

***Rumohra adiantiformis* (Dryopteridaceae):** *Rumohra* species are medium-sized mostly epiphytic or terrestrial ferns that sometimes are considered to be related to *Polystichum* because of their peltate indusia (Hoshizaki & Moran 2001). *Rumohra* species, however, are generally easily recognized by their long-creeping, densely scaly rhizomes with fronds borne in two rows, deltate usually thick-textured decompound blades, and non-spinulose segment margins (Hoshizaki & Moran 2001).

Rumohra adiantiformis, a leathery evergreen perennial, is believed to be indigenous to South America (e.g., Argentina, Bolivia, Brazil, Chile, Peru, Uruguay, and Venezuela), the Greater Antilles, South Africa, Madagascar, Mauritius in the Indian Ocean, Australia, Papua New Guinea, New Zealand, and Tasmania (Lorence 1978; Proctor 1989; Mickel & Smith 2004; ABRS 2018; Kessler et al. 2018). It was not documented for Mesoamerica by Davidse et al. (1995), and the single collection from Jalisco, Mexico, may represent an escape from cultivation (Mickel & Smith 2004).

Rumohra adiantiformis grows in moist to wet forests commonly as a vigorous epiphyte, often on rotting trunks, tree ferns, and a variety of host trees, on rocks, and occasionally as a terrestrial plant (Duncan 1994; ABRS 2018). In Jamaica, Proctor (1985) reported it on trees and rotten logs, rarely in humus-filled pockets of limestone cliffs, widespread in forested regions but mostly rare or uncommon. It can tolerate sandy or loam soils of either poor or good fertility, long periods of dryness, and cool conditions, including frosts (Garrett 1996). Owing, in part, to its coriaceous fronds, *R. adiantiformis* is able to resist desiccation (Lorence 1978).

Cultivated as an ornamental groundcover or grown in pots, *R. adiantiformis* is also prized by florists for its long-lasting cut-fronds used for floral arrangements (Hoshizaki & Moran 2001; De Souza et al. 2006). It is one of the most economically important ferns and is propagated widely for the horticultural industry (Thomas 1999). Both wild and cultivated *R. adiantiformis* are highly variable, but

the peltate indusia become black when mature, robust long-creeping rhizomes, and the leathery leaves allow for easy identification (Hoshizaki & Moran 2001).

Rumohra adiantiformis has naturalized in subtropical and Mediterranean regions, including Florida in the United States and Europe (Verloove 2006; Randal 2017; Wunderlin et al. 2018). USDA, NRCS (2018) reported *R. adiantiformis* is native to Florida. However, others consider these occurrences to be introductions (Lellinger 1985; Wunderlin et al. 2018) as they often grow in suburban woodlands, disturbed areas, and along roadsides (Weakley 2015). *Rumohra adiantiformis*, however, has not naturalized in the Hawaiian Islands (Imada 2012; Vernon & Ranker 2013; USDA, NRCS 2018).

The known locations documented for *R. adiantiformis* growing outside of cultivation in southern California are depicted in Figure 2. It is epiphytic on *Phoenix canariensis*, rarely on *Butia capitata*, entirely within the influence of irrigation facilities. Its epiphytic habitat on *P. canariensis* and distinctive indusia are depicted in Figure 5, Photographs A–B.

***Sphaeropteris cooperi* (Cyatheaceae) new to the California mainland coast:** *Sphaeropteris* Bernh. is native to the American tropics, India, southeastern Asia, Australia, New Zealand, and the Pacific Islands (Hoshizaki & Moran 2001). *Sphaeropteris cooperi* (syn., *Cyathea cooperi* [Hook. ex F. Muell.] Domin) is a medium to large, fast growing tree fern (to 12 m tall) that is native to the subtropical rainforests of eastern Australia (ABRS 2018). It grows along forest margins, steamsides, gullies, and many open habitats, mostly in the coastal lowlands (McCarthy 1998).

Because of its fast growth rate, hardiness, and aesthetic appeal, *S. cooperi* is the most frequently cultivated tree fern in many temperate, subtropical, and tropical regions around the world, including Hawai‘i, California, and elsewhere (Hoshizaki & Moran 2001; Brenzel 2012; Imada et al. 2018). *Sphaeropteris cooperi* is widely known for its adaptability to a variety of soil types, substrates, vegetation communities, tolerance to cold weather or extreme heat, with elevations ranging from sea level to nearly 1,400 m (Large & Braggins 2004; Hoshizaki & Moran 2001; Robinson et al. 2010). In the Hawaiian rainforests, *S. cooperi* is primarily terrestrial (77%), but 20% of the populations studied also grow on fallen logs, and 3% of the occurrences grow as epiphytes (Medeiros et al. 1992).

Sphaeropteris cooperi is known to escape cultivation and has naturalized in temperate, subtropical, and tropical regions around the world, including California, Florida, Oregon, and Hawai‘i in the United States, the Azores and Madeira in Europe, New Zealand, southwest Australia (outside its native range), South Africa, Mauritius, and numerous Pacific Islands (Lorence 1978; Medeiros et al. 1992; Wood 2008; Rosatti 2013; Baard & Kraaij 2014; Randall 2017; ABRS 2018; Euro+Med PlantBase 2018; NZPCN 2018; USDA, NRCS 2018). In Hawai‘i, *Sphaeropteris cooperi* is a serious threat to native ecosystems (Simberloff & Rejmánek 2011). This species aggressively invades natural areas, alters habitats, and out-competes native species, including native tree ferns, *Cibotium* spp. (Medeiros et al. 1992; Durand & Goldstein 2001; Palmer 2003). Displacement of the native tree ferns also alters the composition of epiphyte communities (Medeiros et al. 1993). *Sphaeropteris cooperi* is also invasive in South Africa (Baard & Kraaij 2014).

On the west coast of the United States, *S. cooperi* was first reported outside of cultivation in coastal southern Oregon (Wood 2008), and subsequently on Santa Catalina Island, southern California (Clark & Summers 2013). On Santa Catalina Island, *S. cooperi* grows on exposed granitic and sandstone cliffs in microhabitats that accumulate water, but also on dry, barren rock faces seemingly unsuitable for a species native to wet climates (Clark & Summers 2013). Accordingly, the dry microhabitat seen on Santa Catalina Island and the summer-dry Mediterranean climate in southern California represent conditions generally believed to be inhospitable for naturalization of a tree fern native to subtropical environments

(Durand & Goldstein 2001; Clark & Summers 2013). *Sphaeropteris cooperi* can survive a wide range of conditions, especially with adequate water, so it is expected to spread further in California (Rosatti 2013).

Many epiphytic populations for *S. cooperi* documented outside of cultivation on the California mainland grow on upper palm tree trunks that are not associated with direct irrigation waters. Because of recurrent severe drought, some epiphytic populations may not persist, especially following trimming of palm fronds that exposes plants to the desiccating effects of direct sunlight. *Sphaeropteris cooperi* is epiphytic primarily on *Phoenix canariensis*, rarely on *Butia capitata*. The known epiphytic locations of *S. cooperi* documented for southern California are depicted in Figure 2. Its epiphytic habitat on the upper trunks of *P. canariensis* is depicted in Figure 5, Photographs C–D.

Representative voucher specimens (duplicates to be distributed; data for many additional collections available at Consortium of California Herbaria)**—U.S.A.: CALIFORNIA: Los Angeles Co.:** City of Santa Monica, Pacific Palisades, Bay Club Dr. at Pacific Coast Hwy., 34.04187N -118.54614, elev. ca. 16 m, locally common, epiphyte on the trunk of *Phoenix canariensis*, urban landscape, irrigation spray drift present, 25 Nov 2017, *Riefner 17-543* (UC); City of Malibu, along Pacific Coast Hwy. at Ramirez Mesa Dr., uncommon epiphyte, upper trunk of *Phoenix canariensis*, plants under drought stress, urban landscape, 34.02254N -118.79080W, elev. ca. 30 m, 25 Nov 2017, *Riefner 17-546* (photographic documentation). **Orange Co.:** City of Dana Point, adventive in retail nursery, Pacific Coast Hwy., Ruby Lantern and San Mareno Place, 33.46628N -117.705127W, elev. ca. 49 m, under ledge of concrete block wall, not intentionally planted, irrigation runoff present, growing with *Soleirolia soleirolii*, 17 Feb 2016, *Riefner 16-50* (UC); City of Laguna Beach, Ruby Street Park, 33.52614N -117.76953W, elev. ca. 16 m, rare epiphyte on upper trunk of cultivated *Phoenix canariensis*, 4 Sep 2018, *Riefner 18-113* (photographic documentation); City of Laguna Beach, Glenneyre St. near Center St., 33.52896N -117.76996W, elev. ca. 40 m, two plants epiphytic on upper trunk of cultivated *Phoenix canariensis*, 15 Sep 2018, *Riefner 18-120* (photographic documentation). **San Diego Co.:** City of Carlsbad, along Highland Dr. at Carlsbad Village Dr., 33.16587N -117.33770W, elev. ca. 48 m, business plaza landscape, epiphytic on upper trunk of *Phoenix canariensis* with *Nephrolepis cordifolia*, beyond influence of urban irrigation waters, 20 Nov 2015, *Riefner 15-447* (photographic documentation); City of Carlsbad, N of Batiquitos Lagoon, end of Merlo Ct. and Piovana Ct. off Gabbiano Ln., 33.09621N -117.30136N, elev. ca. 22 m, epiphyte mostly on upper trunks of *Phoenix canariensis*, cultivated street trees, 11 Nov 2017, *Riefner 17-524* (UC).

Noteworthy Epiphytic Species: *Nephrolepis cordifolia* and *Psilotum nudum* have been reported previously from California (Riefner & Smith 2015; Farrar 2018). However, neither species has been reported from California by the USDA, NRCS (2018).

***Nephrolepis cordifolia* (Nephrolepidaceae):** *Nephrolepis cordifolia* is terrestrial, epiphytic, or epilithic. It grows in moist to wet shady places, rain forests, coastal shrublands, wetland and riparian habitats, on epiphyte perches and particularly on palm trunks, limestone ledges and other cliff and rock outcrop habitats, urban areas, old home sites, roadsides, or waste places in Florida, Mexico, West Indies, Central America, South America, Africa, Europe, Southeast Asia, the Pacific Islands and Hawai‘i, Australia, New Zealand, and elsewhere (Nauman 1993b; Hovenkamp & Miyamoto 2005; Randall 2017; ABRS 2018; NZPCN 2018; Euro+Med PlantBase 2018; USDA, NRCS 2018).

In southern California, outside of cultivation *N. cordifolia* has been documented from riparian habitats and on coastal cliff and rock outcrops in native plant communities, but it occurs more frequently in urban environments (Riefner & Smith 2015; CCH 2018).

Representative voucher specimens (duplicates to be distributed; data for many additional collections available at Consortium of California Herbaria)**—U.S.A.: CALIFORNIA: Los Angeles Co.:** City of Los Angeles, E of Westwood Blvd. and W Overland Ave., N side of I-10 Freeway, 34.03206N -

118.41783W, elev. ca. 70 m, epiphyte on trunk of *Phoenix canariensis* cultivated on freeway landscape, 5 Sep 2016, *Riefner 16-364* (UC); City of Malibu, along Pacific Coast Hwy. at Ramirez Mesa Dr., uncommon epiphyte on the upper trunk of *Phoenix canariensis*, growing with *Sphaeropteris cooperi* beyond influence of irrigation sprays, urban landscape, 34.02254N -118.79080W, elev. ca. 30 m, 25 Nov 2017, *Riefner 17-547* (photographic documentation). **Orange Co.:** City of Laguna Beach, W side of El Toro Rd., N of Canyon Hill Dr., 33.59639N -117.74883W, elev. ca. 112 m, uncommon, epiphyte on trunk of *Phoenix canariensis*, within irrigation spray zone, urban landscape, 3 Nov 2017, *Riefner 17-511* (UC); City of Laguna Beach, Glenneyre St. near Diamond St., 33.52837N -117.76919W, elev. ca. 40 m, abundant, epiphytic on upper trunk of cultivated *Phoenix canariensis*, growing with *Asparagus* sp., beyond influence of irrigation waters, 15 Sep 2018, *Riefner 18-121* (photographic documentation). **San Diego Co.:** City of Carlsbad, Highland Dr. at Carlsbad Village Dr., 33.16587N -117.33770W, elev. ca. 48 m, business plaza landscape, epiphytic on upper trunk of *Phoenix canariensis* with *Sphaeropteris cooperi*, beyond influence of urban irrigation waters, 20 Nov 2015, *Riefner 15-448* (photographic documentation); City of San Diego, Mission Valley, Hotel Circle South, vicinity of Taylor St., 32.75910N -117.181768W, elev. ca. 12 m, epiphytic on upper trunk of *Phoenix canariensis* beyond influence of urban irrigation waters, business plaza landscape, 14 Jan 2017, *Riefner 17-22* (photographic documentation); City of San Diego, Point Loma, along Catalina Blvd. near Pio Pico St., 32.71473N -117.24773W, elev. ca. 97 m, epiphytic on upper trunk of cultivated *Phoenix canariensis*, beyond influence of urban irrigation waters, roadside landscape, 16 Jun 2018, *Riefner 18-74* (photographic documentation).

The known epiphytic occurrences for *N. cordifolia* documented outside of cultivation are depicted in Figure 6, including the populations reported previously by Riefner and Smith (2015) and CCH (2018). Its preferred host tree is *Phoenix canariensis*, but *N. cordifolia* is also epiphytic on *Butia capitata*, *Washingtonia robusta*, and rarely on *Pinus pinea* L. (Pinaceae). Spontaneous populations have been recorded within the spray zone of irrigation facilities, but it also grows high on trunks and into the crowns of palm trees beyond the influence of irrigation waters. Its epiphytic habitat on *P. canariensis* and *B. capitata* and distinctive morphological features are depicted in Figure 7, Photographs A–E.

***Psilotum nudum* (Psilotaceae):** *Psilotum nudum* is a terrestrial or epiphytic perennial with short-creeping, rhizoid-bearing rhizomes with aerial stems to 50 cm tall (Mickel & Smith 2004; Diggs & Lipscomb 2014). It is widespread in warm-temperate, subtropical, and tropical regions of the Americas, Asia, Africa, Australia, New Zealand, and the Pacific Islands (Thieret 1993; Mickel & Smith 2004). *Psilotum nudum* grows in low mesic woods, rain forests, wet montane forests, rocky slopes, thickets, swamps, hammocks, old logs, or epiphytic at the bases of trees, tree forks, and in leaf detritus in urban gardens, 0-1,500 m elevation (Thieret 1993; Mickel & Smith 2004; Diggs & Lipscomb 2014). It is also a minor greenhouse weed (Thieret 1993).

In the United States and its territories, *P. nudum* occurs in North Carolina south to Florida and west to Arkansas, Louisiana, Texas, and Arizona, and in Puerto Rico, the Virgin Islands, and Hawai‘i (Thieret 1993; Imada 2012; Diggs & Lipscomb 2014; Weakley 2015; USDA, NRCS 2018). In California, *P. nudum* apparently was introduced, likely on root masses as subterranean gametophytes (Farrar 2018). It is cultivated occasionally in greenhouses (CCH 2018). Although *P. nudum* has been reported previously by several authors (Roberts et al. 2004; Clarke et al. 2007; Dean et al. 2008; Roberts 2008), it has been omitted for California by the USDA, NRCS (2018).

Representative voucher specimens (duplicates to be distributed; data for many additional collections available at Consortium of California Herbaria)—**U.S.A.: CALIFORNIA: Los Angeles Co.:** City of Los Angeles, San Pedro, West 37th St. at South Dolphin St., 33.71484N -118.30736W, elev. ca. 44 m, locally abundant, epiphytic on the lower trunk of *Phoenix canariensis,* growing with *Nephrolepis cordifolia*, urban landscape, irrigation spray present, 26 Mar 2016, *Riefner 16-79* (UC). **Orange Co.:** City of Costa Mesa, E side of Orange County Fairground, Lot #A-5, W of Newport Blvd. and N of Fair Dr.,

33.66540N -117.89807W, elev. ca. 32 m, epiphytic on lower trunks of *Syagrus romanzoffiana* in irrigated planters, 22 Nov 2015, *Riefner 15-453* (UC). **San Diego Co.:** City of La Jolla, Village of La Jolla, Kline St. at Herschel Ave., 32.84387N -117.27260W, elev. ca. 38 m, epiphytic on lower trunk of *Syagrus romanzoffiana* in irrigated urban landscape, 14 Jan 2017, *Riefner 17-26* (UC).

The known epiphytic occurrences documented for *P. nudum* outside of cultivation in southern California are depicted in Figure 6. All documented populations are associated with irrigation facilities, where it grows at the base of *Phoenix canariensis* or *Syagrus romanzoffiana*.

***Cyrtomium falcatum* (Dryopteridaceae): First Report for Epiphytic Behavior:** *Cyrtomium falcatum* is terrestrial or epilithic in its native and introduced range, but it also grows epiphytically in southern California's urban forests. We regard it as an accidental epiphyte, following the classification scheme of Zotz (2016).

Cyrtomiums are terrestrial, evergreen, perennial ferns native to tropical and subtropical regions distributed primarily in East Asia, but centered in southwest China (Zhang & Barrington 2013). The genus *Cyrtomium* is taxonomically difficult and not easily separated from *Polystichum* (Mickel & Smith 2004; Diggs & Lipscomb 2014). In the wild, species of *Cyrtomium* grow in soil or on rocks, not as epiphytes; a few facultative epiphytic species are known for *Polystichum* (Hoshizaki & Moran 2001; Zotz 2016). *Cyrtomium falcatum* is native to the coastal lowland forests of Indochina, Japan, Korea, and Polynesia (Zhang & Barrington 2013).

Widely escaped from cultivation, *C. falcatum* has naturalized in Europe, the Azores and Macaronesia, North America, Hawai'i, Madagascar, Reunion, South Africa, Australia, New Zealand, and elsewhere (Roux 2011; Imada 2012; Zhang & Barrington 2013; Randall 2017; ABRS 2018; Euro+Med PlantBase 2018; NZPCN 2018; USDA, NRCS 2018). In the continental United States, *C. falcatum* has naturalized primarily in the southeast, but occurrences have been reported for the Pacific Northwest, Mid-Atlantic, and Northeastern States (Yatskievych 1993; Weakley 2015; USDA, NRCS 2018). It grows on urban masonry, mesic cliffs, ravines, and rock outcrops, coastal bluffs, riparian habitats, and on streambanks (Smith 2012a; Diggs & Lipscomb 2014; Weakley 2015). For California, DiTomaso and Healy (2007) described it as occasionally naturalized without significant ecological or economic damage, possibly under-collected or overlooked. *Cyrtomium falcatum* now has been documented from diverse habitats over a broad geographical range for California (Smith 2012a; CCH 2018).

Cyrtomium falcatum is apomictic and can produce genetically variable progeny (Lollyd & Davis 1994; Smith 2012a). Juvenile sporophytes of apogamous species mature quickly, which can be advantageous in dry regions with a short growing season (Robinson et al. 2010). Thus, colonization of new sites, including water-stressed habitats, is facilitated by apogamous reproduction (Grusz 2016). During this study, small and somewhat fleshy fertile plants (<15 cm fronds) were collected on palm trunks and coastal bluffs (*Riefner 18-37*, *18-106*, *18-109*; UC). BGCI (2018) listed 'Maritimum' and other miniature *C. falcatum* cultivars that might be referable to these populations. However, we cannot, with certainty, assign a name to these plants; 'dwarfness' may be dictated by extreme growing conditions in a Mediterranean climate—a niche facilitated by the apogamous breeding system of the species.

Representative voucher specimens (duplicates to be distributed; data for many additional collections available at Consortium of California Herbaria)—**U.S.A.: CALIFORNIA: Los Angeles Co.:** City of Malibu, Eastern Malibu, N side Pacific Coast Highway at Carbon Mesa Rd., W of Carbon Canyon Rd., 34.03905N -118.6539W, elev. ca. 31 m, rare epiphyte on *Phoenix canariensis,* growing with *Nephrolepis cordifolia*, urban landscape, irrigation spray present, 13 Dec 2015, *Riefner 15-471* (UC). **Orange Co.:** City of Newport Beach, Corona del Mar, along Marguerite Ave. near Seaview Ave., 33.59523N -117.87203W, elev. ca. 30 m, epiphytic on upper *Phoenix canariensis* tree trunk, uncommon,

growing with *Ficus rubiginosa*, beyond the influence of irrigation waters, 27 Aug 2015, *Riefner 15-365* (photographic documentation); City of Laguna Beach, Aliso Beach Park, W of Coast Highway, 33.50984N - 117.75135W, elev. ca. 4 m, dwarf plants uncommon, fleshy, epiphytic on trunks of *Phoenix canariensis* cultivated along parking lot, 24 Mar 2018, *Riefner 18-37* (UC). **San Diego Co.:** City of Del Mar, Coast Blvd. at 21st St., 32.96690N -117.267585W, elev. ca. 4 m, epiphytic on upper *Phoenix canariensis* tree trunk, uncommon, growing with *Solanum* sp., beyond influence of irrigation waters, 1 Feb 2017, *Riefner 17-50* (photographic documentation); City of Carlsbad, N side of Agua Hedionda Lagoon, along Adams St., E of Highland Dr., 33.14519N -117.32581W, elev. 15 m, uncommon, epiphytic on the trunks of *Phoenix canariensis*, cultivated street trees, 30 Jun 2017, *Riefner 17-324* (UC).

The epiphytic occurrences documented for *C. falcatum* in southern California are depicted in Figure 6. Populations have been recorded mostly within the spray zone of irrigation facilities, but plants also grow on upper palm tree trunks beyond the influence of irrigation waters. Its epiphytic habitat on *Phoenix canariensis* and distinctive morphologies are depicted in Figure 8, Photographs A–D.

DISCUSSION

Until recently, urban ecosystems have received little attention from scientists (Daily & Ehrlich 1999). Urban forests are one of the most complex and dynamic components of urban ecosystems (Chen & Jim 2008), yet their biodiversity remains poorly studied (Alvey 2006; Nagendra & Gopal 2011; Threlfall et al. 2016). Thus, urban ecology is a rapidly emerging discipline and urban ecosystems have become legitimate topics for study (Pickett et al. 2001).

For southern California, we document eight epiphytic fern species reproducing spontaneously in urban settings. Our findings suggest that urban forest ecosystems are promoting non-native epiphytes by facilitating interactions between a preferred cultivated phorophyte, *Phoenix canariensis*, and several epiphytic ferns escaping cultivation. Urban irrigation waters, supplemented by coastal fog drip, provide moisture during the dry summers, which in part, enable the subtropical-tropical ferns escaping cultivation to establish and disperse spontaneously in arid southern California. With recurrent severe drought, escalating costs, and inherent cut-backs for irrigation waters, the epiphytic ferns documented here are primarily species adapted to drought-prone environments.

Phoenix canariensis: The Preferred Urban Forest Phorophyte

The abundance and species richness of vascular epiphytes is often higher on palms than on non-palm tree hosts (Akinsoji 1990; Aguirre et al. 2010). *Phoenix canariensis* and other species of palms with marcescent leaf bases (withering but not falling off the trunk) promote the accumulation of detritus (i.e., arboreal humus) in axils of old leaf bases that favor epiphyte colonization (Putz & Holbrook 1989; Kramer 2011; Bhatt et al. 2015). See Wagner et al. (2105) for a review.

In Mediterranean climates, which are characterized by low irregular annual rainfall and high temperatures (mild wet winters and hot dry summers), vascular epiphytes can be scarce (Torrecillas et al. 2013). However, in semiarid climates some species of palms are known to support epiphytes, such as *Phoenix canariensis* or *P. dactylifera* (Torrecillas et al. 2013). In its native habitat, the Canary Islands, *P. canariensis* is a well-known host that supports an astonishing diversity of epiphytes (Morici 1998). Interestingly, Morici (1998) also noted that *P. canariensis* trees cultivated along the historic Palm Avenue in urban Camino Largo, La Laguna, Tenerife, are also colonized by epiphytes. In addition, Brandes (2007) observed that *P. canariensis* is an important phorophyte for epiphyte colonization along the Mediterranean Sea: i.e., Gozo, Malta; Dalmatia, Croatia; Italy; and Sousse, Tunisia.

Phoenix canariensis tolerates a wide range of conditions, and worldwide is one of the most widely cultivated of all palms (Morici 1998; Zona 2008). It is also popular in southern California (Hatch 2007; Ritter 2011). Based on previous studies (Riefner & Smith 2015; Riefner 2016), reports from other Mediterranean regions, host tree architecture that promotes the accumulation of detritus and thus microhabitat resource availability, the frequency of cultivation, and the data complied during this study point to *P. canariensis* as the preferred urban forest phorophyte in coastal southern California.

Spontaneous Epiphytic Ferns: Casual Urban-Dwellers or Potential Invasive Species

Worldwide, one of the most important pathways for the introduction and dispersal of invasive plants is escape from horticulture (Reichard & White 2001; Dehnen-Schmutz et al. 2007; Faulkner et al. 2016). Urban gardens contain numerous non-native plants that are offered for sale from the ornamental horticulture industry (Raloff 2003; Pergl et al. 2016). Although most ornamentals can survive only where intentionally cultivated, some escape without human assistance (Mayer et al. 2017). Thus, cities are often hotspots of introduction and invasion where non-native ornamental plants escape gardens and disperse to surrounding environments (Gaertner et al. 2017; Mayer et al. 2017). Pteridophytes are no exception.

The eight non-native epiphytic ferns documented in this study are cultivated (Hoshizaki & Moran 2001). Four of them, *Cyrtomium falcatum*, *Nephrolepis cordifolia*, *Rumohra adiantiformis*, and *Sphaeropteris cooperi* are popular cultivated ferns (Brenzel 2012; TFF 2018). Ornamental ferns escaping cultivation disperse spontaneously by natural means, primarily by wind-blown spores originating from mature sporulating plants. Thereby, ferns introduced by horticulture and escaping gardens may represent an important colonization pathway for the epiphytic invasion of southern California's urban forests.

Although some non-native species thrive in urban habitats, they may not spread beyond city environments and/or impact biodiversity and ecosystem functions of native ecosystems (Cadotte et al. 2017). *Nephrolepis cordifolia* (Riefner & Smith 2015) and *Sphaeropteris cooperi* (Clark & Summers 2013), for example, were first reported growing outside of cultivation from California's native plant communities. However, both species volunteer spontaneously and are more widely distributed in urban environments than native habitats. Conversely, *Cyrtomium falcatum* is well-documented from native habitats (Smith 2102a), but rarely reported from urban environments (CCH 2018).

At numerous urban forest sites in southern California, aerosol sprays from irrigation facilities benefit ferns growing on the lower trunks of palm trees. However, *Cyrtomium falcatum*, *Nephrolepis cordifolia*, and *Sphaeropteris cooperi* flourish on upper palm tree trunks well beyond the influence of irrigation waters. For the summer-dry Mediterranean California climate, this epiphytic treetop habitat seemingly is unsuitable for ferns native to mesic or wet climates. Clark and Summers (2013) suggested a persistent marine layer and fog drip may have facilitated the unlikely naturalization of *Sphaeropteris cooperi* on Catalina Island cliffs in an area of relatively high exposure with little apparent moisture. Much like the cliff habitat, the epiphytic ferns documented on upper trunks of palm trees grow in a microclimate characterized by little apparent moisture and the desiccating effects of summer heat.

Characteristic fogs and overcast along the California coast, colloquially known as 'June gloom' (Wikipedia 2018b), are consistently associated with coastal Mediterranean regions where the fog season coincides with the dry season (Schemenauer & Cereceda 1991; Burgess & Dawson 2004; Fischer et al. 2009). Persistent summer fog can increase available moisture and low stratus clouds provide shade that reduces evapotranspiration and solar radiation, which alleviate plant drought stress during the rainless summers (Burgess & Dawson 2004; Williams et al. 2008; Fischer et al. 2009; Chung et al. 2017). These and other variables such as host tree architecture and bark characteristics (Wagner et al. 2015), and the nutrient status of arboreal humus (Putz & Holbrook 1989) also influence epiphyte performance.

Globally, few obligate epiphytes are invasive (Zotz 2016; Randall 2017). Invasiveness is a feature of some non-native organisms having life history traits and modes of reproduction that enable them to overcome normal barriers to invasion (Richardson et al. 2011). In Table 2, we compare our preliminary epiphytic classifications with drought-tolerance traits, native habitat occurrences, and the Global Risk Score for each species listed by Randall's (2017) *Global Compendium of Weeds*. None of these epiphytic ferns has been rated for California by Cal-IPC (2018).

Table 2. Comparison of California Adventive Ferns for Observed Epiphytic Class, Drought Tolerance, Native Habitat Occurrences, and Invasive Risk Potential.

Species	Epiphytic Class	Drought Tolerance	Documented Native Habitat(s)	Global Risk Score (GRS)
Davallia solida	Obligate	Sheds fronds or parts of blades during dry seasons	Wildland-urban interface epiphyte	—
Phlebodium aureum	Obligate	Sheds fronds seasonally during drought	—	GRS: 2.88 Rating: Low
Phlebodium pseudoaureum	Obligate	Sheds fronds seasonally, desiccation-tolerant gametophytes	—	—
Rumohra adiantiformis	Obligate	Coriaceous fronds resist desiccation	—	—
Sphaeropteris cooperi	Facultative	Unknown	Cliff and rock outcrops, wildland-urban interface epiphyte	GRS: 4.32 Rating: Low
Nephrolepis cordifolia	Facultative	Water stored in tubers, vegetative reproduction by wiry stolons	Cliff and rock outcrops, terrestrial in riparian habitats, wildland-urban interface epiphyte	GRS: 9.60 Rating: Medium
Psilotum nudum	Facultative	—	—	—
Cyrtomium falcatum	Accidental	Apomictic reproduction, precocious maturation of dwarf plants in harsh habitats	Cliff and rock outcrops, terrestrial in riparian habitats, littoral zones	GRS: 5.76 Rating: Low

Jones et al. (2018) conducted a global assessment for terrestrial non-native ferns to determine species' traits that influence naturalization and invasion. They identified 11 species of concern, including four species that we document here, namely *Cyrtomium falcatum*, *Nephrolepis cordifolia*, *Phlebodium aureum*, and *Sphaeropteris cooperi*.

CONCLUSIONS

Urban ecosystems are often underexplored, but they contain some of the most unique and interesting assemblages of species observed anywhere around the world (Francis & Chadwick 2015). The study of biological invasions, however, has only recently paid attention to urban environments (Jarošík et al. 2011; van Ham et al. 2013; Gaertner et al. 2017). Accordingly, the rising interest in urban ecosystems has been accompanied by a global surge in scientific publications and a paradigm shift in attitude—from the urban as unnatural, to the urban as interesting and ecologically important (Kowarik 2011; Wu 2014; McDonnell 2015; Salomon Cavin & Kull 2017).

Invasive ornamental species, in general, have received less attention when they do not directly invade natural communities (Geerts et al. 2017). In southern California, documentation of urban plant invasions has largely been ignored in favor of wildland habitat invasive species; in either case little attention has been given to the pteridophytes. Ferns have often been portrayed as mesic-loving plants. However, emerging studies documenting desiccation-tolerance of free-living gametophytes, in combination with highly dispersible spores of the sporophytes, facilitate the adaptation and colonization by ferns to new and often drought-prone habitats, including previously unexpected urban forest environments in arid southern California.

Additionally, there is a need for greater exploration of the socio-ecological-economic values for spontaneous urban plants of southern California. The aesthetically pleasing ferns should be part of this discussion (Morajkar et al. 2015). Southern California's interesting and attractive urban-dwelling ferns represent a prime subject for further research. We encourage others to explore and investigate the epiphytic ferns in our urban environments.

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Figure 1. Urban forest, southern California: **A**–view from I-5 Freeway looking towards the Pacific Ocean showing the diversity of trees planted along city streets, business plazas, and residential housing tracts, City of San Clemente, Orange County, California; **B**–*Phoenix canariensis* and *Washingtonia robusta* cultivated in a greenbelt, City of Malibu, Los Angeles County, California; **C**–*P. canariensis* cultivated along public streets, City of San Diego, Point Loma, San Diego County, California; **D**–*P. canariensis* and *W. robusta* cultivated in coastal park, City of Laguna Beach, Orange County, California.

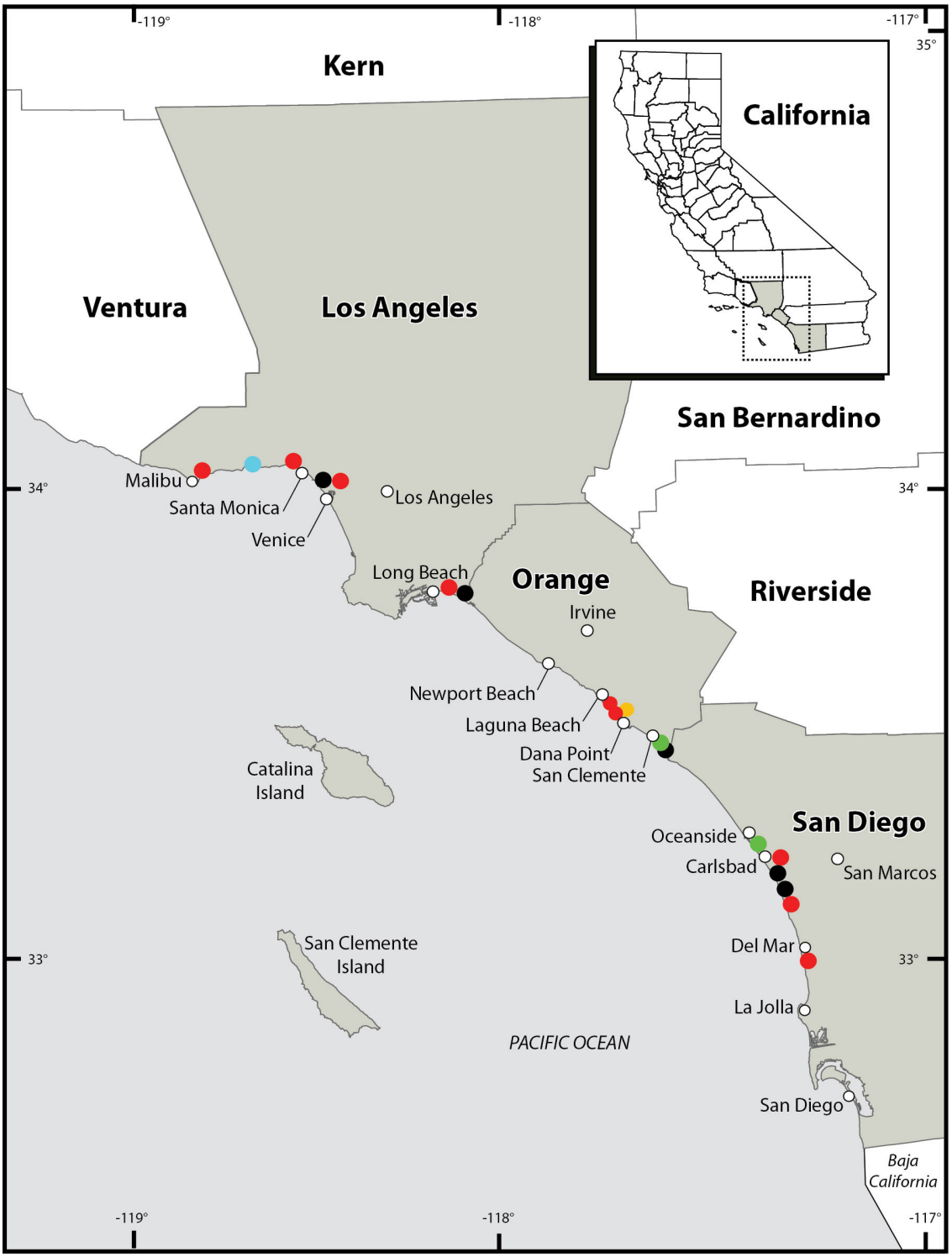

Figure 2. Known epiphytic occurrences for *Davallia solida* (●), *Phlebodium aureum* (●), *Phlebodium pseudoaureum* (●), *Rumohra adiantiformis* (●), and *Sphaeropteris cooperi* (●) documented outside of cultivation in southern California's urban forests.

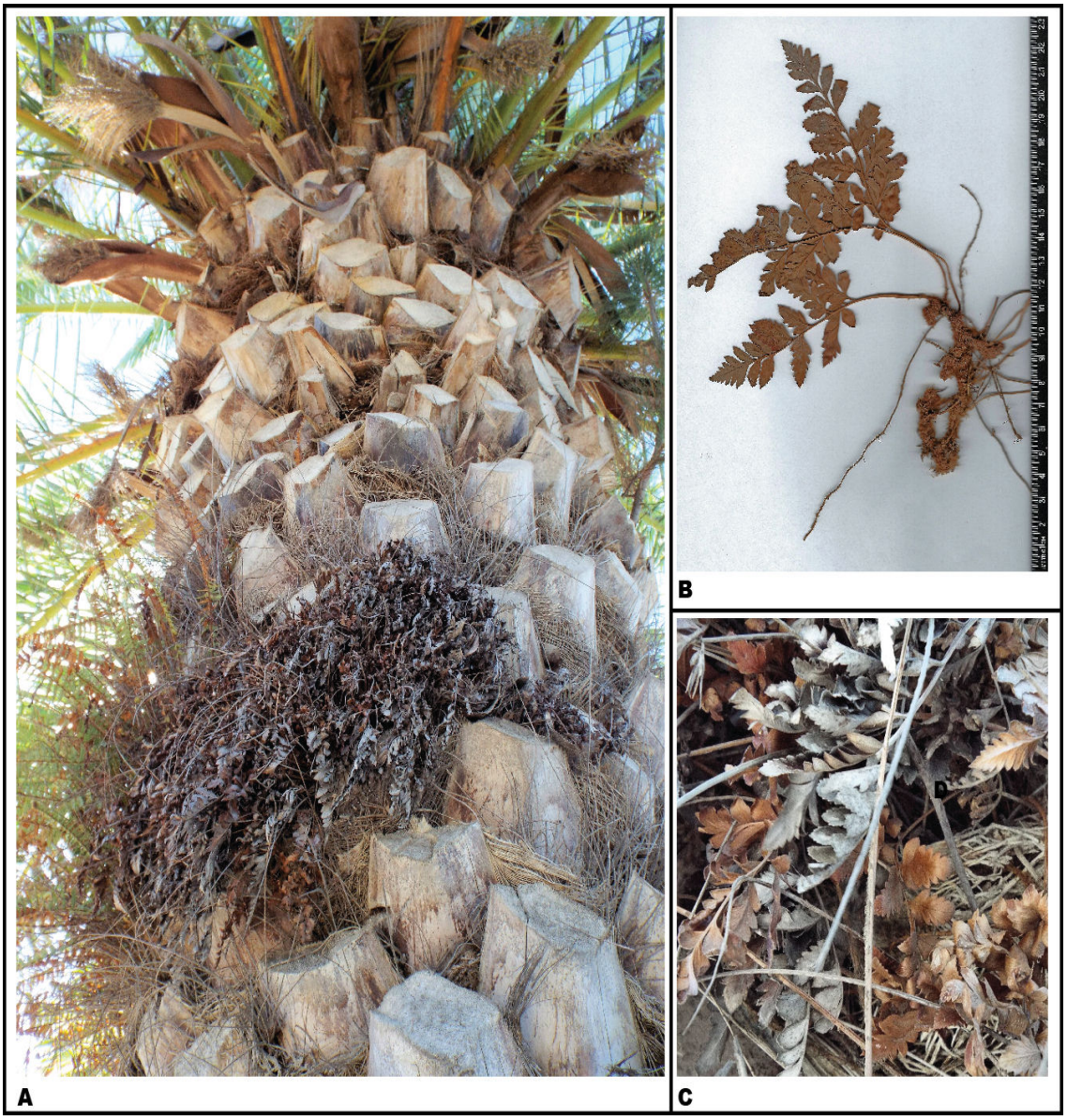

Figure 3. *Davallia solida* (Oceanside, California; *RR 16-385* UC): **A**–epiphytic habitat on *Phoenix canariensis* cultivated along a public street, photographs taken during summer drought, note on far left side of trunk is drought-stressed *Nephrolepis cordifolia*; **B**–scan showing small frond size and long-creeping scaly rhizomes, scale in cm; **C**–close-up showing portions of lamina shed during periods of drought.

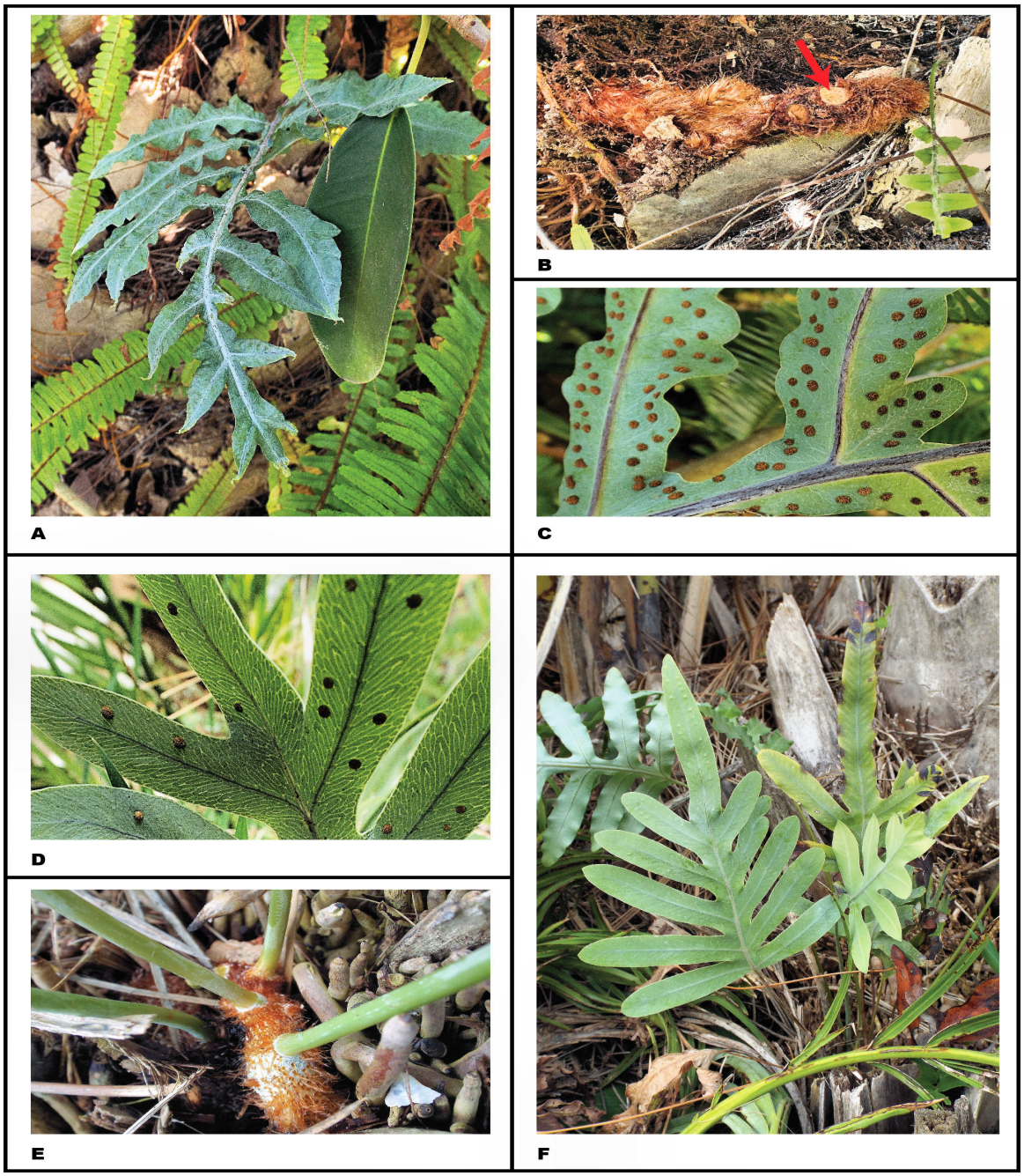

Figure 4. *Phlebodium aureum* (Malibu, California; *RR 15-469* UC): **A**–epiphytic habitat on *Phoenix canariensis* cultivated in public greenbelt, photo depicting young frond, deeply lobed with narrow segments growing with *Nephrolepis cordifolia* and *Ficus rubiginosa*; **B**–robust long-creeping rhizome with golden-brown scales, note phyllopodia (red arrow) and juvenile *N. cordifolia* frond; **C**–abaxial view of fertile frond showing sori arranged in two rows between the costa and pinna margin.

Phlebodium pseudoaureum (Laguna Beach, California; *RR 18-110* UC): **D**–abaxial view of fertile frond showing sori arranged in a single row between the costa and pinna margin and distinctive venation; **E**–creeping, pruinose rhizomes with lanceolate orange-colored scales; **F**–epiphytic habitat on *Phoenix canariensis* cultivated in park greenbelt, note deciduous fronds in lower left-hand portion of the photo.

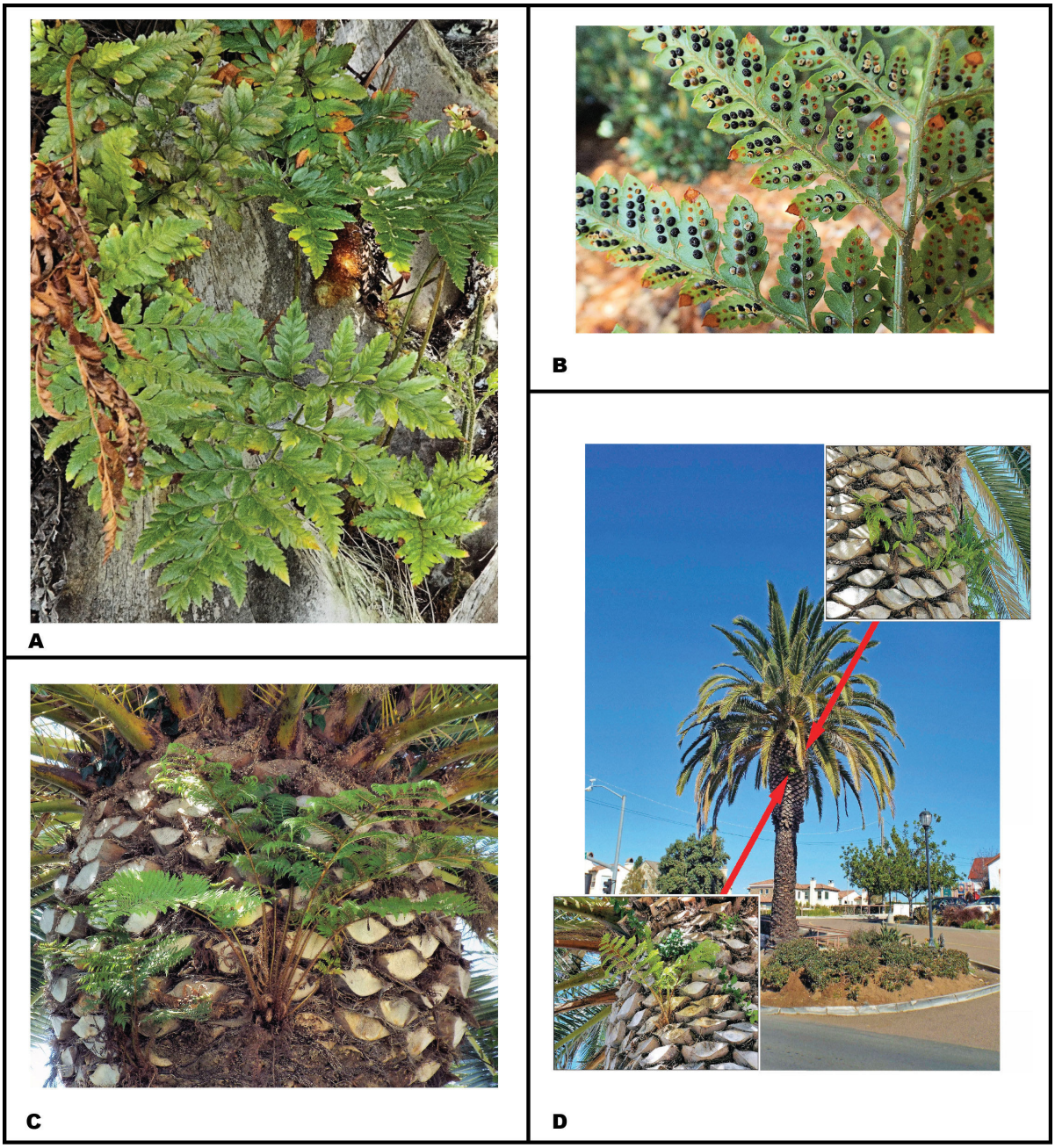

Figure 5. *Rumohra adiantiformis* (Carlsbad, California; *RR 17-52* UC): **A**–epiphytic habitat on *Phoenix canariensis* cultivated in neighborhood greenbelt; **B**–abaxial frond view showing peltate indusia that turn black and form an upside-down cup when mature.

Sphaeropteris cooperi: **C**–epiphytic habitat on upper trunk of *P. canariensis* cultivated in residential neighborhood (Laguna Beach, California; *RR 18-120* photographic voucher); **D**–epiphytic habitat on *P. canariensis* cultivated in business plaza (Carlsbad, California; *RR 15-447* photographic voucher), lower left inset close-up of upper trunk plants and upper right inset a close-up of plants growing with *Nephrolepis cordifolia* (*RR 15-448* photographic voucher).

Figure 6. Known epiphytic occurrences for *Cyrtomium falcatum* (●), *Nephrolepis cordifolia* (●), and *Psilotum nudum* (●) documented outside of cultivation for southern California's urban forests.

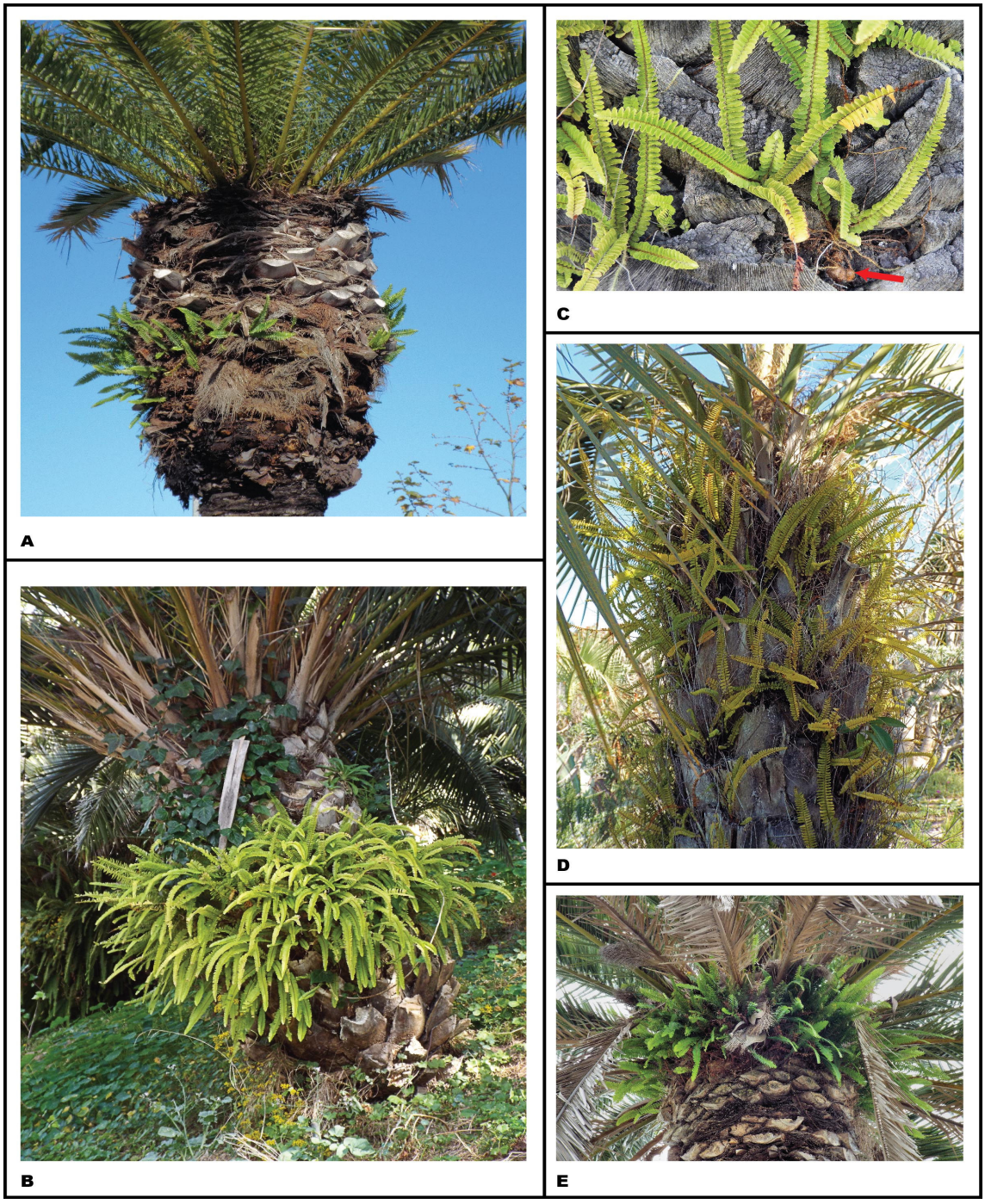

Figure 7. *Nephrolepis cordifolia*: **A**–epiphytic habitat on upper trunk of *Phoenix canariensis* cultivated in business plaza (Mission Valley, California; *RR 17-22* photographic voucher); **B**–on *P. canariensis* cultivated in greenbelt (Santa Monica, California; *RR 17-541* UC); **C**–on *Butia capitata* cultivated along coastal promenade, red arrow points to tubers (Long Beach, California; *RR 14-258* UC); **D**–on *B. capitata* cultivated in residential neighborhood, note *Ficus microcarpa* seedling on lower right trunk (Encinitas, California; *RR 16-13* UC); **E**–on upper trunk of *P. canariensis* cultivated along public street (Point Loma, California; *RR 18-74* photographic voucher).

Figure 8. *Cyrtomium falcatum*: **A**–*Phoenix canariensis* epiphytic habitat, tree cultivated in county park greenbelt (Laguna Beach, California; *RR 18-39* UC); **B**–small size and precocious maturation may facilitate survival on palms in a Mediterranean climate (Laguna Beach, California; *RR 18-38* UC); **C**–*P. canariensis* epiphyte assemblage with *Ficus rubiginosa* on cultivated street tree, inset photo showing *C. falcatum* growing on upper palm trunk (Newport Beach, California; *RR 15-365* photographic voucher); **D**–epiphytic on upper trunk of *P. canariensis* cultivated along public street (Del Mar, California; *RR 17-50* photographic voucher).