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# Population assessment and conservation strategies for the Critically Endangered lichen *Sulcaria isidiifera*

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ABSTRACT: The epiphytic lichen *Sulcaria isidiifera* is a critically imperiled species endemic to the coast of central California, USA, where it occupies just a few patches of old-growth maritime chaparral habitat. *S. isidiifera* has experienced major habitat loss due to urban development, while facing ongoing threats from wildfires, land conversion, and climate change. In 2019, *S. isidiifera* was listed on the IUCN Red List. The Red List assessment recommended that the species be monitored to track abundance, reintroduced where extirpated, and listed as an endangered species in the USA. Our study aimed to follow up on recommended conservation actions by characterizing occupied habitat, obtaining comprehensive abundance data, and performing a translocation experiment. Population data collected during our study resulted in estimates of 13 841–25 064 individuals growing on 3588–7772 host shrubs distributed across a range of 24 km$^2$. *S. isidiifera* was more abundant in areas exhibiting greater winter-to-summer swings in relative humidity. The foliose lichen *Leucodermia leucomelos* was identified as an indicator species for *S. isidiifera*. To determine whether the IUCN recommendation of reintroducing *S. isidiifera* to previously occupied habitat is feasible, we translocated individuals of *S. isidiifera* to nearby putative suitable habitat and monitored their health using chlorophyll fluorescence. After 3.5 yr, we report 92% survival of translocated individuals with no notable negative impacts on their health. The population size and restricted range of this species indicate that management activities like translocation, and Endangered Species Act listing are warranted to conserve *S. isidiifera*.

KEY WORDS: Climate Change · Endangered Species · IUCN Red List · Lichens

## 1. INTRODUCTION

Lichens are symbiotic organisms comprising a fungal partner (mycobiont) and one or more photosynthetic partners (photobionts) that form the thallus (Grimm et al. 2021, Allen & Lendemer 2022). This symbiotic relationship is one of the reasons why lichens are able to thrive in a wide range of habitats and are often viewed as ecosystem pioneers (Kolita & Gogoi 2024). Poikilohydry, the ability of lichens to halt metabolic activity when dry, also allows them to tolerate desiccation, which further increases their range of potential habitats (Kranner et al. 2008). While lichens are seemingly ubiquitous, they are

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understudied and often overlooked in conservation efforts (Allen & Lendemer 2015, Davoodian 2015, Allen et al. 2019). Lichens play an important role in many ecosystems by regulating nutrient and water availability, facilitating soil development, and serving as food, shelter, nesting material, and camouflage for other organisms (Gerson & Seaward 1977, Pypker et al. 2006, Delgado-Baquerizo et al. 2015, Zavarzina et al. 2019, Grimm et al. 2021).

While legal conservation frameworks exist in many countries, they rarely apply to lichens. A few exceptions include Canada (Species at Risk Act), the UK (Wildlife and Countryside Act 1981), Norway (Nature Diversity Act), and Iceland (Advertisement on the protection of vascular plants, mosses and lichens), which explicitly include lichens in their enacted legislation. In the USA, the federal Endangered Species Act (ESA) is recognized as affording some of the strongest legal protections globally for threatened species; however, the ESA only protects 2 lichen species: the rock gnome lichen *Cetradonia linearis* (=*Gymnoderma lineare*) (A. Evans) J.C. Wei & Ahti and the Florida perforate lichen *Cladonia perforata* A. Evans. This represents just 0.1% of the 3800 lichen species that are estimated to occur in the USA (Allen et al. 2019).

For other groups of organisms, particularly plants and animals, methods for conserving rare and threatened species are relatively well studied, with translocation efforts for threatened animals documented prior to the 20th century (Novak et al. 2021). For lichens, translocation for the purpose of conservation only began to occur in the latter half of the 20th century (Smith 2014). Yet the need to develop lichen conservation methods has never been greater, as populations are declining due to anthropogenic impacts including urbanization, increased wildfire frequency and intensity, air pollution, and climate change (Miller et al. 2018, Allen et al. 2019, Ellis & Coppins 2019, Esseen et al. 2022, Mueller et al. 2022).

The splitting yarn lichen *Sulcaria isidiifera* Brodo is among the rarest and most narrowly endemic lichen species in North America and faces multiple anthropogenic threats to its survival. *S. isidiifera* is an epiphytic, fruticose lichen that is 3–5 cm in length and is only known to reproduce asexually via vegetative propagules called isidia (Brodo 1986). It occurs on the central coast of California in small patches of old-growth California maritime chaparral (hereafter maritime chaparral) habitat (Carlberg & Knudsen 2007). This habitat supports 2 narrowly endemic plants: *Arctostaphylos morroensis* Wies. & Schreib. (Morro manzanita) and *Eriodictyon altissimum* P.V. Wells (Indian Knob mountainbalm); and one animal, *Helminthoglypa walkeriana* Hemphill (Morro shoulderband snail). Much of this habitat has been destroyed or degraded by the development of the unincorporated Los Osos community in San Luis Obispo County (Carlberg & Knudsen 2007). The remaining occurrences of *S. isidiifera* are located on several properties separated by urban development. Maritime chaparral habitat occurs in other areas of coastal California; however, to date, *S. isidiifera* has never been documented outside of San Luis Obispo County (Consortium of Lichen Herbaria 2025). In 2019, the International Union for Conservation of Nature (IUCN) listed *S. isidiifera* on its Red List of Threatened Species as Critically Endangered B2ab (i,ii,iii,iv,v) due to a decline in the number of mature individuals and major threats to the population, including residential and commercial development, natural ecosystem modifications such as fire and fire suppression, climate change, and severe weather (McMullin et al. 2019). While this listing characterized the distribution and threats to *S. isidiifera*, it did not assess the population in detail. The assessment also relied on the relatively sparse data that are available from herbarium records and historical observations of *S. isidiifera*. Nonetheless, conservation actions were recommended, including listing *S. isidiifera* as an endangered species in the USA, reintroducing individuals to previously occupied habitat, and monitoring to ascertain the abundance and health of the species.

In the present study, we addressed a suite of pressing conservation research needs for *S. isidiifera*. We completed the first empirical, comprehensive assessment of the population size, and created a more detailed map of the species' distribution. We then characterized the microclimate, vegetation community, and associated lichen community of *S. isidiifera*-occupied habitats. We also developed and tested translocation methods to build an additional conservation action tool for this species. The conservation translocation allowed us to test 3 hypotheses: (1) host phorophyte species affects thallus health; (2) individuals placed on north sides of shrubs will fare better than individuals placed on the south sides; and (3) individuals placed closer to the ground will fare better than individuals placed higher up on host shrubs. The latter 2 hypotheses are proposed due to higher levels of humidity on the north sides of shrubs and on branches closer to the ground. The goal of testing these hypotheses is to inform future conservation translocation efforts by determining the most suitable microclimate for *S. isidiifera*.

## 2. MATERIALS AND METHODS

### 2.1. Study area

The study area includes the communities of Los Osos and Baywood Park, which are located on the central coast of California. The study area is characterized by a Mediterranean climate with mild, dry summers and cool, wet winters. Fog is common year-round and is often present in the mornings but dissipates by the afternoon. Mean annual precipitation is 400 mm (2005–2022; San Luis Obispo County Public Works). During the same 2005–2022 time period, mean daily temperatures ranged from 9.9 to 17.9°C (PRISM Climate Group 2023). The study area is located on an ancient dune complex of Baywood fine sands. Protected lands in the study area include Montaña de Oro State Park, Los Osos Oaks State Reserve, Morro Bay State Park, Morro Dunes Ecological Reserve, and the El Moro Elfin Forest.

### 2.2. Population assessment

To assess the current range and population size of *Sulcaria isidiifera*, we researched and cataloged all known localities of *S. isidiifera* (Consortium of Lichen Herbaria 2023, R. E. Riefner pers. comm.) and plotted them in a web-based geospatial application (AmigoCloud). These data allowed for both targeted surveys of suitable habitat within the mapped range of the species and surveys in adjacent maritime chaparral habitat outside of this range (Fig. 1). Surveys for potentially suitable habitat for *S. isidiifera* were carried out between November 2020 and May 2022 over the course of 11 survey days. An additional meandering survey was

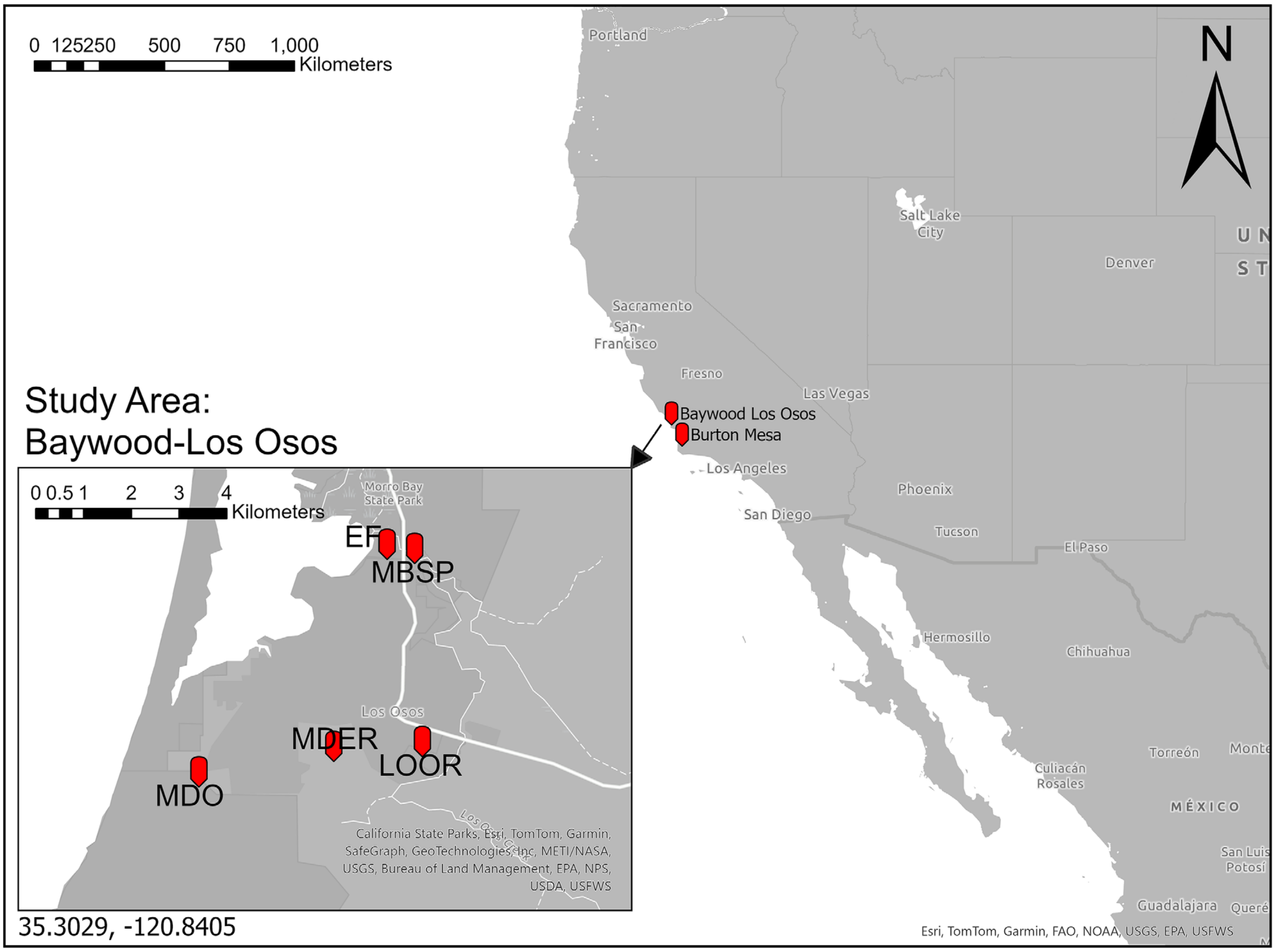


Fig. 1. Study area; inset displays 5 main sites where *Sulcaria isidiifera* surveys occurred, along with the location of the additional meandering survey at Burton Mesa Ecological Reserve. Study sites (top to bottom): El Moro Elfin Forest (EF), Morro Bay State Park (MBSP), Morro Dunes Ecological Reserve (MDER), Los Osos Oaks State Reserve (LOOR), and Montaña de Oro State Park (MDO)

performed in Burton Mesa Ecological Reserve on 10 September 2022 to determine whether this disjunct stand of maritime chaparral contained *S. isidiifera*.

Meandering transect surveys were conducted in areas known to contain *S. isidiifera* to map host shrubs containing the species. High-resolution aerial imagery was captured via drone to create orthomosaic maps to aid in vegetation type analysis. Key survey areas were then defined in ArcGIS and divided into 8000 $m^2$ subsections, which were broken down to 10 m wide pedestrian transects (Fig. 2). For complete population counts, surveyors searched for *S. isidiifera* one subsection at a time by walking each transect line. Each suitable host shrub was searched for *S. isidiifera*. Litterfall on the ground beneath each host plant was searched for detached thalli. Binoculars were also used to search for *S. isidiifera* in areas inaccessible on foot. The area of occupancy (AOO) and extent of occurrence (EOO) were calculated according to the Guidelines for Using IUCN Red List Categories and Criteria (IUCN Standards and Petitions Committee 2022). The EOO is defined as the area contained within the shortest continuous imaginary boundary that can be drawn to encompass all the known occurrences of a taxon, while the AOO is the area within the EOO that is actually occupied by a taxon (IUCN Standards and Petitions Committee 2022).

Both functional individuals and the number of mature individuals were counted. Functional individuals refer to the number of occupied host shrubs (Yahr et al. 2024). Mature individuals are defined by the IUCN as individuals capable of reproduction (IUCN Standards and Petitions Committee 2022). We assigned a unique, randomly generated identifier to each functional individual and recorded the date, time, and observer's name. Functional individuals located on the

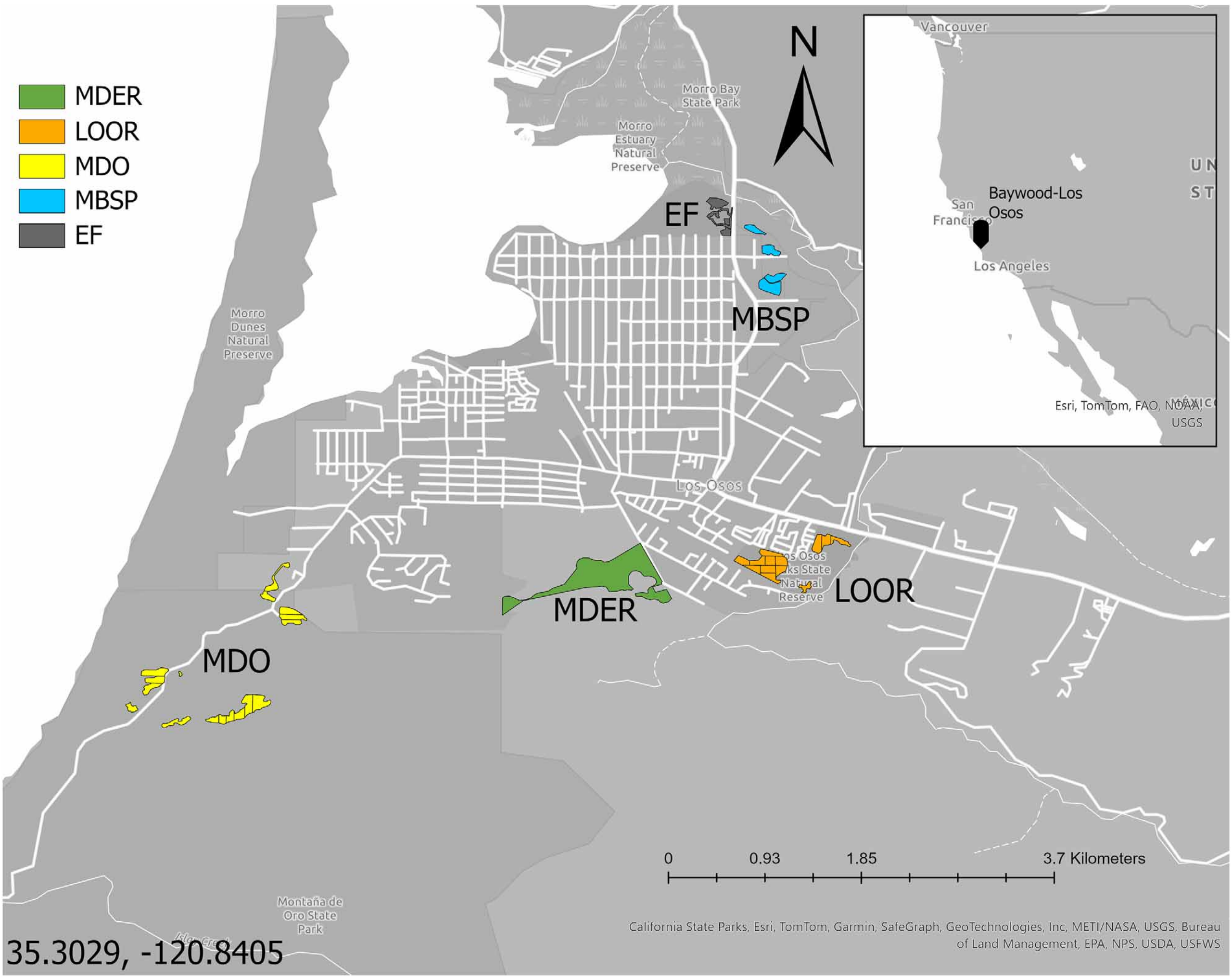


Fig. 2. Key survey areas identified as *Sulcaria isidiifera* habitat in Montaña de Oro State Park (MDO), Morro Dunes Ecological Reserve (MDER), Los Osos Oaks State Park (LOOR), the El Moro Elfin Forest (EF), and Morro Bay State Park (MBSP)

boundary between 2 survey areas were marked and noted to prevent duplicate counts. For each subsection, the start and stop times were recorded as well as the surveyor(s) initials. Population density was calculated using the minimum bounding geometry tool in ArcGIS Pro to create a minimum convex polygon around each disjunct portion of the population. Within each polygon that was defined, the population density was calculated. Even though *S. isidiifera* was not distributed evenly throughout its range, the estimated population density should be considered accurate, given that each minimum convex polygon encompassed primarily undisturbed and suitable habitat for this species.

For stands of vegetation that were inaccessible to surveyors due to the density of shrubs, line transects were placed 15 m apart along the boundary of the stand, with the starting point of the transects randomly placed. Along each transect, three 2 × 2 m quadrats were placed at 10 m intervals and were surveyed for *S. isidiifera*. The spacing of quadrats allowed for quadrat data to be collected separately near the edge and the interior of each stand to facilitate comparisons of population density of *S. isidiifera* at these positions. A total of 15 quadrats were surveyed at each location in Morro Dunes Ecological Reserve, Montaña de Oro State Park, and the El Moro Elfin Forest, totaling 45 quadrats among all sites. Estimates of additional individuals were determined by calculating the population density of *S. isidiifera* within quadrats and extrapolating to the whole stand. Stand sizes were determined in ArcGIS Pro using drone imagery. Using this approach, 2 estimates of additional *S. isidiifera* individuals were calculated. A conservative estimate accounted for individuals only in the stands where transect surveys occurred. The second, liberal estimate accounted for additional individuals potentially present in adjacent but inaccessible habitat that we deemed suitable for *S. isidiifera* based on vegetation composition and proximity to other individuals.

### 2.3. Ecological assessment

In addition to identifying the vascular plant vegetation communities occupied by *S. isidiifera*, we characterized lichen community assemblages and microclimate within maritime chaparral habitat occupied by *S. isidiifera* at a local scale. Lichen community surveys were conducted between March and September 2022. To capture lichen community composition on host branches, we used a different quadrat approach in which a total of 60 quadrats were randomly placed in or near stands of vegetation occupied by *S. isidiifera* on host shrub branches. Each quadrat had a surface area of 200 $cm^2$, calculated using the formula for the lateral surface area of a conical frustum: 1/2 × (Circumference 1 + Circumference 2) × length (Hobbs 1921). Once calculated, the quadrat area was delineated using flagging tape, and the entire surface of the branch within each quadrat was examined (Fig. 3). A total of 12 quadrats were placed at each of the 5 study sites: Morro Dunes Ecological Reserve, Montaña de Oro State Park, El Moro Elfin Forest, Morro Bay State Park, and Los Osos Oaks State Reserve.

Within each site, 6 quadrats were randomly placed within the boundaries of occupied *S. isidiifera* habitat. Random points were established and then used to search for the nearest *S. isidiifera* host plant, and that host was sampled. The remaining 6 quadrats were selected using the same methods with random points but were placed in adjacent habitat that did not contain *S. isidiifera*. These quadrat locations were selected to match the features of one of the previously selected quadrats within *S. isidiifera* habitat, such that each pair comprised one sample with *S. isidiifera* and one without.

Once a shrub was selected, quadrats were established on a randomly selected branch. Branches were considered suitable based on the presence or absence of *S. isidiifera* and for their accessibility. For the 6 quadrats within *S. isidiifera* habitat, the first easily accessible branch found with *S. isidiifera* was se-

Fig. 3. Example of a 200 $cm^2$ branch quadrat used to quantify epiphyte community composition on host shrubs. Green flagging tape marks the boundary of the quadrat

lected. The remaining 6 quadrats were then selected so that they were located at least 30 m away from *S. isidiifera* habitat and so that each pair had the same host species, aspect, branch height above ground, and branch circumference. For each quadrat, the percent cover for each macrolichen species (i.e. foliose or fruticose growth forms; McCune & Geiser 2009) was determined using the Braun-Blanquet cover-abundance scale. The percent cover of microlichens (crustose and related growth forms; McCune 2017) and other organisms (e.g. mosses and non-lichenized fungi) was also determined, but individual species were not identified. Lichens that could not be identified in the field were collected and determined in a laboratory using dissecting microscopy, chemical spot tests, and dichotomous keys (Brodo et al. 2001, McCune & Geiser 2009, McCune & Yang 2019). Vouchers of all lichen species identified were deposited into OBI, the Robert F. Hoover Herbarium at Cal Poly State University.

To determine whether temperature and relative humidity (RH) are limiting factors in the establishment and growth of individuals on similar hosts in nearby chaparral communities, we characterized the microclimate of *S. isidiifera*. In total, 14 temperature and humidity sensors (DS1923 Hygrochron Temperature/Humidity iButton, Analog Devices; DROP D2 Wireless Temperature & Humidity Data Logger, Kestrel) were deployed in and near *S. isidiifera* habitat. Microclimate was measured for 1 yr between September 2021 and September 2022. The sensors were affixed to branches using nylon monofilament fishing line. Given that the housings for the Hygrochron sensors are permeable to water, they were waterproofed using a clear rubber coating. This coating prevented water damage without compromising the accuracy of the temperature and humidity readings. A small cut was made in the rubber coating around the humidity sensor that allowed ambient humidity to be measured. Four of the Kestrel microclimate sensors were deployed in adjacent habitat on randomly selected shrubs without *S. isidiifera*. Temperature and RH were recorded every 3 h beginning at 00:00 h.

To evaluate whether the use of different temperature and humidity sensors may have yielded different values, we compared their outputs using ANOVA before deployment, which indicated no significant difference in temperature readings. The Kestrel sensors did provide significantly lower humidity readings than the iButtons ($F$ = 8.618, df = 1, p = 0.00341), but the difference was consistent across each individual reading, such that the overall trends and differences were not affected.

### 2.4. Translocation trial

A total of 30 *S. isidiifera* thalli were randomly selected, translocated, and monitored between 27 May 2021 and 16 November 2024. This relatively small sample size was chosen to reduce potential impacts on the *S. isidiifera* population. One thallus was also found on the ground and was determined to be a viable candidate for translocation. Individuals were selected by placing randomized points within habitat known to be occupied by *S. isidiifera*. The nearest individual to that point was selected while matching thallus size and maturity as well as the density of isidia among individuals. We targeted thalli 5–9 cm in length and avoided those exhibiting necrotic areas. For each individual collected, the thallus was photographed alongside a photomicrographic scale (Fig. 4), and we recorded the thallus height above ground, host species, and aspect of the host shrub on which it was found.

Of the 30 thalli, 24 were translocated and distributed between 2 new host shrub species, *Adenostoma fasciculatum* Hook. & Arn. and *Arctostaphylos morroensis*, in adjacent suitable habitat unoccupied by *S. isidiifera* (Fig. 5). The new host shrubs were randomly selected and were chosen because they are known hosts for *S. isidiifera* (Consortium of Lichen Herbaria 2023). The remaining 6 individuals of *S. isidiifera*


Fig. 4. *Sulcaria isidiifera* thallus used as part of the translocation experiment, pictured alongside a photomicrographic scale. Photographs were taken of each thallus after it was removed from its host shrub

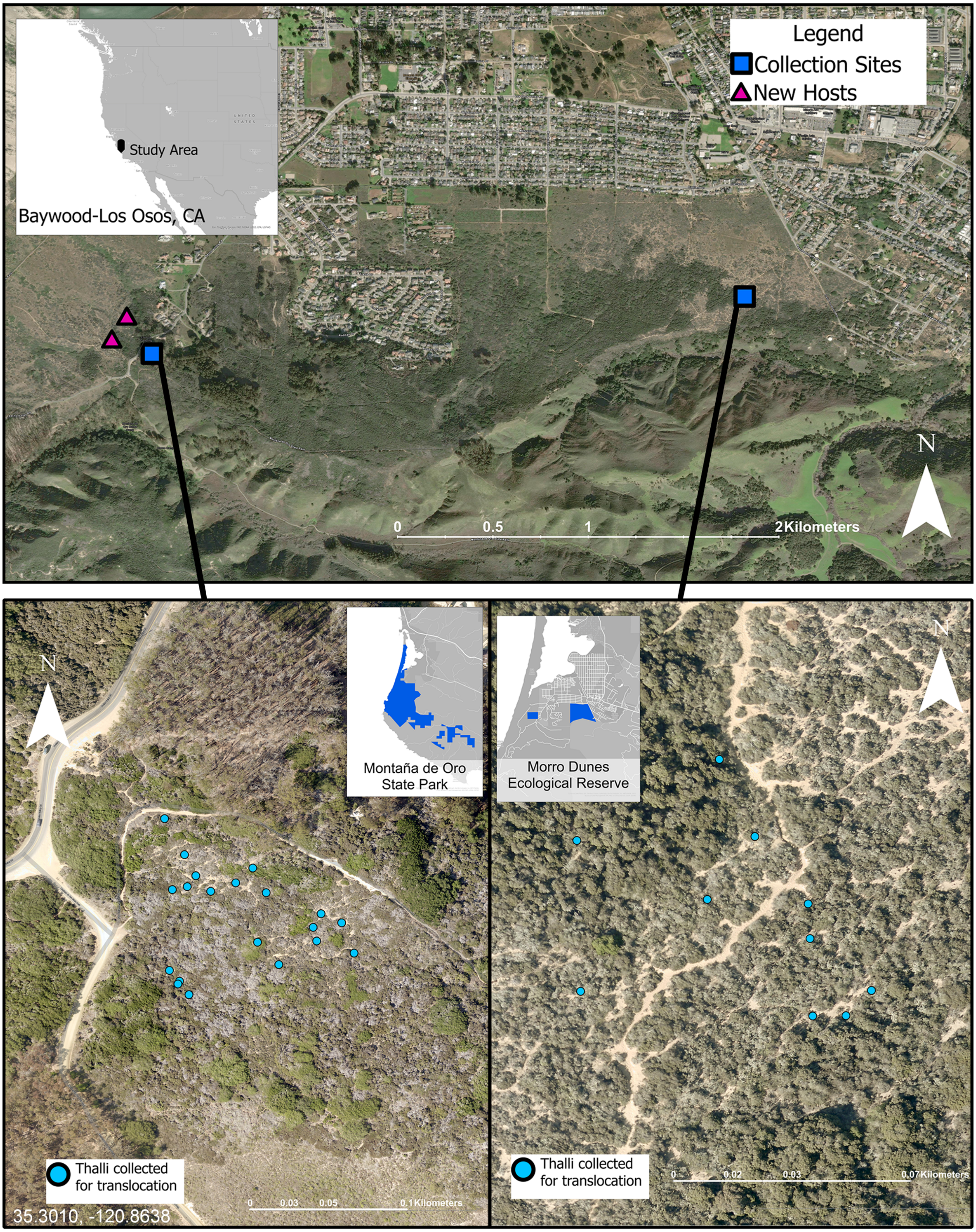


Fig. 5. Top: sites where *Sulcaria isidiifera* thalli were collected (dark blue squares) and subsequently translocated (pink triangles). Bottom: collection sites in Montaña de Oro State Park (left) and Morro Dunes Ecological Reserve (right)

served as a control group in that they were removed from their host shrubs, transported with the experimental thalli, and then re-attached to their original host shrubs.

To minimize impacts to thalli, all individuals were collected in brown paper bags, placed in a clear plastic tub, and relocated the same day that they were collected. We also reduced the potential for incidental damage by clipping and translocating whole intact branch sections on which *S. isidiifera* was growing. Each sample was then re-attached to the new substrate using a combination of nylon fishing line and epoxy (Araldite 2-part epoxy) on the branch, being careful to avoid contact between the epoxy and thallus. To test our hypotheses, experimental thalli were distributed evenly between the *A. fasciculatum* and *A. morroensis* hosts, north and south aspects of shrubs, and 0.5 and 1.0 m above the ground (Fig. 6).

Temperature and RH sensors were placed next to each control thallus in the original collection locations, as well as on the north and south aspect of each shrub that hosted experimental thalli. Temperature and RH were recorded every 3 h, starting at 00:00 h. Light exposure was measured in μmol $m^{-2}$ $s^{-1}$ using a photosynthetically active radiation (PAR) sensor (MQ-100X Quantum Integral Sensor, Apogee Instruments). Light exposure was monitored individually for all 30 thalli, measured at 09:00 h (±30 min), 12:00 h (±30 min), and 15:00 h (±30 min) over the course of a single day, every other month between 30 June 2021 and 30 June 2022. A total of 21 measurements at each location and 126 combined measurements at all locations were taken over the course of 1 yr. To measure PAR, the sensor was placed parallel to the surface of the thallus. For instances in which the thallus was inconsistently shaded, measurements were taken in both the shaded and unshaded portions of the thallus, and the average value was recorded.

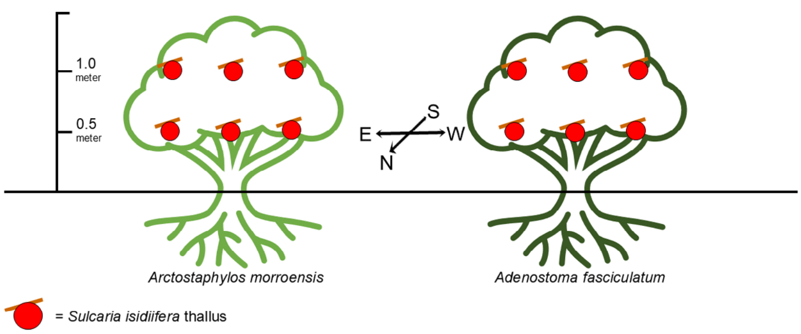


Fig. 6. Simplified diagram of *Sulcaria isidiifera* thallus placement on new host shrubs for a translocation experiment. Six thalli were placed on the north and south aspects of each shrub species at both 0.5 and 1.0 m heights, totaling 24 translocated thalli on 2 host shrubs

To assess the vitality of *S. isidiifera* individuals, chlorophyll *a* fluorescence was measured as a proxy for thallus health (Jensen & Kricke 2002, Paoli et al. 2020, Chekanov & Lobakova 2021). The parameter $F_v/F_m$ (unitless) was used to indicate the maximum photochemical quantum efficiency of photosystem II of the photobiont (Kitajima & Butler 1975). The parameter $F_v$ is determined by first measuring the minimum value for chlorophyll fluorescence ($F_0$) in dark-adapted photobionts, then shortly after the maximum value of chlorophyll fluorescence ($F_m$) when photobionts are exposed to a pulse of light (Murchie & Lawson 2013); $F_v$ is the difference between $F_0$ and $F_m$. Chlorophyll fluorescence was measured using a pulse-modulated chlorophyll fluorescence fluorometer (FMS 2, Hansatech Instruments). Sufficient branches of *S. isidiifera* were gathered together so that the probe end was covered, and an equal thallus surface area was measured in each sample. To ensure that thalli were dark-adapted for measurement, chlorophyll fluorescence was measured at night between 21:45 and 01:15 h on 14 and 15 July 2022. Thalli were sprayed with distilled water 10 min before measuring. Chlorophyll fluorescence measurements were recorded for all 30 thalli in the translocation trial as well as an additional 30 undisturbed thalli that were randomly selected for comparison.

### 2.5. Statistical analyses

Statistical analyses were completed in R (R Core Team 2021). All random points were established using the 'create random points' tool in ArcGIS software. A significance level of $\alpha = 0.05$ was used for all statistical tests. To assess potential differences in *S. isidiifera* population density between transects in inaccessible stands at 10, 20, and 30 m distances from the stand edges, a Kruskal-Wallis rank sum test was performed using the 'kruskal.test' function. To compare species richness and microclimate between lichen communities and microclimate between disjunct portions of the *S. isidiifera* population, ANOVA was completed using the 'aov' function. To confirm homogeneity of variances between sample populations before performing ANOVA, Levene's test was performed using the 'leveneTest' function from the 'car' package (Fox & Weisberg 2019). To determine which of these disjunct areas occupied by *S. isidiifera* had the largest microclimate differences from one another, Tukey's honestly significant difference (HSD) test was completed using the 'tukeyHSD' function. Communities with and without *S. isidiifera* were compared via species richness and diversity across sample sites using the 'vegan' package (Oksanen et al. 2022). We used the Shannon-Wiener index to calculate diversity using the 'diversity' function. To determine whether lichen community composition differed significantly between *S. isidiifera* and non-*S. isidiifera* communities, we constructed a species composition matrix of the presence of species and the relative abundance in each quadrat and converted it into a Bray-Curtis distance matrix that was then subjected to permutational multivariate analysis of variance (PERMANOVA) with 999 permutations, performed with the 'adonis2' function in the 'vegan' package (Oksanen et al. 2022). To visualize differences between *S. isidiifera* and non-*S. isidiifera* communities due to lichen species composition and microclimate, non-metric multidimensional scaling was completed using the 'metaMDS' function. The 'envfit' function was used to quantify how well aligned the abiotic variables were with variation in composition between communities with and without *S. isidiifera*. A multivariate Levene's test was performed using the 'betadisper' function to confirm homogeneity of variances between groups. Indicator species analysis (ISA) was also used to identify lichen taxa that were closely associated with *S. isidiifera*. The 'multipatt' function of the 'Indicspecies' package (De Cáceres & Legendre 2009) was used to perform ISA. Grouping factors for ISA were community type (lichen species composition was compared between *S. isidiifera* habitat and adjacent non-*S. isidiifera* habitat). For the translocation experiment, ANOVA was carried out to compare the microclimate between control and experimental translocation sites. Tukey's HSD test was used to determine which of these sites had the largest differences in microclimate. To compare the potential differences in PAR between the north and south sides of shrubs, the data were plotted, and a smooth curve was applied using the 'geom_smooth' function with the loess method. Finally, we performed Welch's two sample *t*-tests using the 't.test' function to compare the health of (1) translocated and randomly selected, undisturbed thalli that were not removed from their original host; (2) translocated thalli on different host shrub species; (3) thalli on north and south aspects; (4) thalli placed at different heights; and (5) translocated and control thalli.

## 3. RESULTS

### 3.1. Population assessment

A total of 2816 functional individuals, or host shrubs, of *Sulcaria isidiifera* were counted. The number of mature individual thalli counted was 11 549. No individuals were detected outside of the known range of *S. isidiifera* during the survey at Burton Mesa Ecological Reserve on 10 September 2022. Within the observed range of the species, the total area of maritime chaparral habitat occupied by *S. isidiifera* was 1.874 km$^2$, resulting in a density of 6163 thalli km$^{-2}$ and 1503 functional individuals km$^{-2}$. The AOO and EOO were reassessed and calculated to be 24 km$^2$ each. The mean number of thalli per host shrub was 4.09. The maximum number of thalli counted on a single host shrub was 130. Among study sites, the highest number of functional individuals counted was 904, located in Los Osos Oaks State Reserve, and the smallest number of individuals was found in El Moro Elfin Forest, with 328 functional individuals. Population density was highest in Morro Bay State Park and lowest in Montaña de Oro State Park (Table 1).

For stands of vegetation that were inaccessible, 2 estimates were determined. In the more conservative approach, an additional 2840 thalli (±548) and 957 functional individuals (±185) were estimated. A liberal estimate predicted an additional 12 542 thalli

Table 1. Area surveyed, population count, and density of *Sulcaria isidiifera* at El Moro Elfin Forest (EF), Morro Bay State Park (MBSP), Montaña de Oro State Park (MDO), Morro Dunes Ecological Reserve (MDER), and Los Osos Oaks Reserve (LOOR)

| | Property size (km$^2$) | *S. isidiifera* occupied habitat (km$^2$) | No. of functional individuals | No. of thalli | Density (functional ind. km$^{-2}$) | Density (thalli km$^{-2}$) |
|---|---|---|---|---|---|---|
| EF | 0.36 | 0.06 | 328 | 1116 | 5466 | 18600 |
| MBSP | 10.92 | 0.09 | 632 | 3573 | 7022 | 39700 |
| MDO | 32.37 | 1.03 | 499 | 2418 | 484 | 2348 |
| MDER | 1.16 | 0.45 | 453 | 1478 | 1007 | 3284 |
| LOOR | 0.34 | 0.25 | 904 | 2964 | 3616 | 11856 |
| Total | 45.15 | 1.87 | 2816 | 11549 | | |

(±973) and 4604 functional individuals (±352). Within these stands, the number of *S. isidiifera* was not found to be different between 10, 20, and 30 m distances from the stand edges (Kruskal-Wallis $\chi^2$ = 1.8141, df = 2, p = 0.4037). Together with direct count data and the estimated number of *S. isidiifera* in inaccessible stands, the total population size is estimated to be between 13 841 and 25 064 individual thalli and 3588–7772 functional individuals.

### 3.2. Ecological assessment

*S. isidiifera* was observed almost exclusively in maritime chaparral habitat, dominated by *Adenostoma fasciculatum*, *Arctostaphylos morroensis*, and *Ceanothus cuneatus* (Hook.) Nutt. Central and Southern California Coastal Sage Scrub and Coast Live Oak Woodland vegetation communities were also present in the study area, and often intergraded with maritime chaparral habitat. However, *S. isidiifera* was found primarily on mature chaparral shrub species. The most common shrubs on which *S. isidiifera* grew were *A. fasciculatum* (2214 functional individuals), *C. cuneatus* (384 functional individuals), and *A. morroensis* (135 functional individuals). Other less common host species, which comprised a total of 83 functional individuals, included *Artemisia californica* Less., *Quercus agrifolia* Née, and *Salvia mellifera* Greene.

The maritime chaparral lichen community was relatively diverse, with available substrate often densely populated. A total of 25 macrolichen taxa were identified among all quadrats in this study (Table 2); 22 taxa were recorded in *S. isidiifera* habitat and 21 taxa were recorded in non-*S. isidiifera* habitat. Even though the lichen communities overlapped in species composition, they differed significantly (PERMANOVA, $F$ = 2.825, df = 1,58, $R^2$ = 0.046, p = 0.009). Species richness was significantly higher in *S. isidiifera* quadrats, with an average of 6.93 species quadrat$^{-1}$ compared to 5.40 in non-*S. isidiifera* habitat (ANOVA, $F$ = 5.962, df = 1,8, p = 0.017). However, macrolichen diversity, as characterized by the Shannon-Wiener index, did not show a significant difference between communities. The most common macrolichen species identified in the quadrats were *Evernia prunastri* (L.) Ach., *Flavoparmelia caperata* (L.) Hale, *Hypogymnia minilobata* McCune & Schoch., *H. mollis* L.H. Pike & Hale, *Parmotrema perlatum* (Hudson) M. Choisy, *Ramalina farinacea* (L.) Ach., and *Usnea rubicunda* Stirton. *F. caperata*, *P. perlatum*, and *U. rubicunda* covered the greatest portions of branches. Species that commonly co-occurred with *S. isidiifera* were *Leucodermia leucomelos* (L.) Kalb, *Ramalina leptocarpha* Tuck, *S. spi-*

Table 2. List of macrolichen species identified in community surveys. Symbols (×) indicate whether the lichen was present in *Sulcaria isidiifera* habitat and/or non-*S. isidiifera* habitat

| Taxon | *S. isidiifera* habitat | Non-*S. isidiifera* habitat |
|---|---|---|
| *Cladonia* spp. | × | × |
| *Evernia prunastri* (L.) Ach. | × | × |
| *Flavoparmelia caperata* (L.) Hale | × | × |
| *Flavopunctelia flaventior* (Stirt.) Hale | | × |
| *Heterodermia namaquana* Brusse | × | × |
| *Hypogymnia gracilis* McCune | × | × |
| *Hypogymnia heterophylla* L.H. Pike | | × |
| *Hypogymnia inactiva* (Krog) Ohlsson | | × |
| *Hypogymnia minilobata* McCune & C.L Schoch | × | × |
| *Hypogymnia mollis* Pike & Hale | × | × |
| *Kaernefeltia merrillii* (Du Rietz) A. Thell & Goward | × | × |
| *Leucodermia leucomelos* (L.) Kalb | × | × |
| *Niebla cephalota* (Tuck.) Rundel & Bowler | × | × |
| *Parmelia sulcata* Taylor | × | |
| *Parmotrema perlatum* (Huds.) M. Choisy | × | × |
| *Ramalina farinacea* (L.) Ach. | × | × |
| *Ramalina leptocarpha* Tuck. | × | |
| *Ramalina menziesii* Taylor | × | × |
| *Sulcaria isidiifera* Brodo | × | |
| *Sulcaria spiralifera* (Brodo & D. Hawksw.) Myllys, Velmala & Goward | × | |
| *Usnea cornuta* Körb | × | × |
| *Usnea esperantiana* P. Clerc | × | × |
| *Usnea fragilescens* Hav. ex Lynge | × | × |
| *Usnea perplexans* Stirt. | × | × |
| *Usnea rubicunda* Stirt. | × | × |

*ralifera* (Brodo & D. Hawksw.) Myllys, Velmala & Goward, and *U. fragilescens* Hav. ex Lynge. In addition, *L. leucomelos* was found to be a significant indicator species for *S. isidiifera* habitat according to ISA (p = 0.042).

During the study period from September 2021 through September 2022, microhabitat temperatures were relatively moderate in *S. isidiifera* sites, with averages ranging from 10°C in the winter to 16°C in the summer. Over the course of the year, the highest average daily maximum temperature observed was during fall at around 20°C. The lowest average daily minimum temperature was during winter at around 7°C. During the same time period, RH ranged from 76% in the fall to just under 86% in the summer. The highest and lowest average daily maximum RH were observed during summer (98%) and fall (79%), respectively. RH was significantly different between the different sites occupied by *S. isidiifera* and, in general, higher values of humidity during fall and winter months correlated with a higher density of *S. isidiifera* thalli and functional individuals (Fig. 7).

Conversely, the correlation was negative during the summer, where higher RH areas had a lower density of *S. isidiifera* (linear regression, $R^2 = 0.898$, $F = 2.09 \times 10^4$, $p < 0.001$). When comparing *S. isidiifera* and non-*S. isidiifera* communities, maximum humidity (ANOVA, $F = 40.23$, df = 1, $p = 0.012$), minimum humidity ($F = 147$, df = 1, $p = 0.008$), and minimum temperatures ($F = 3.035$, df = 1, $p = 0.027$) were significantly different (Fig. 8).

### 3.3. Translocation trial

Visual observations and chlorophyll fluorescence measurements were gathered for translocated thalli at the conclusion of the 13.5 mo trial. A subsequent visual monitoring event occurred on 16 November 2024, when 2 thalli on exposed branches were not found, resulting in a survival rate of 92% after 3.5 yr. The latter visual assessment showed little to no change in the color or size of thalli. However, we did observe growth of thallus branches onto the host substrate for one individual. During this event, 4 thalli,

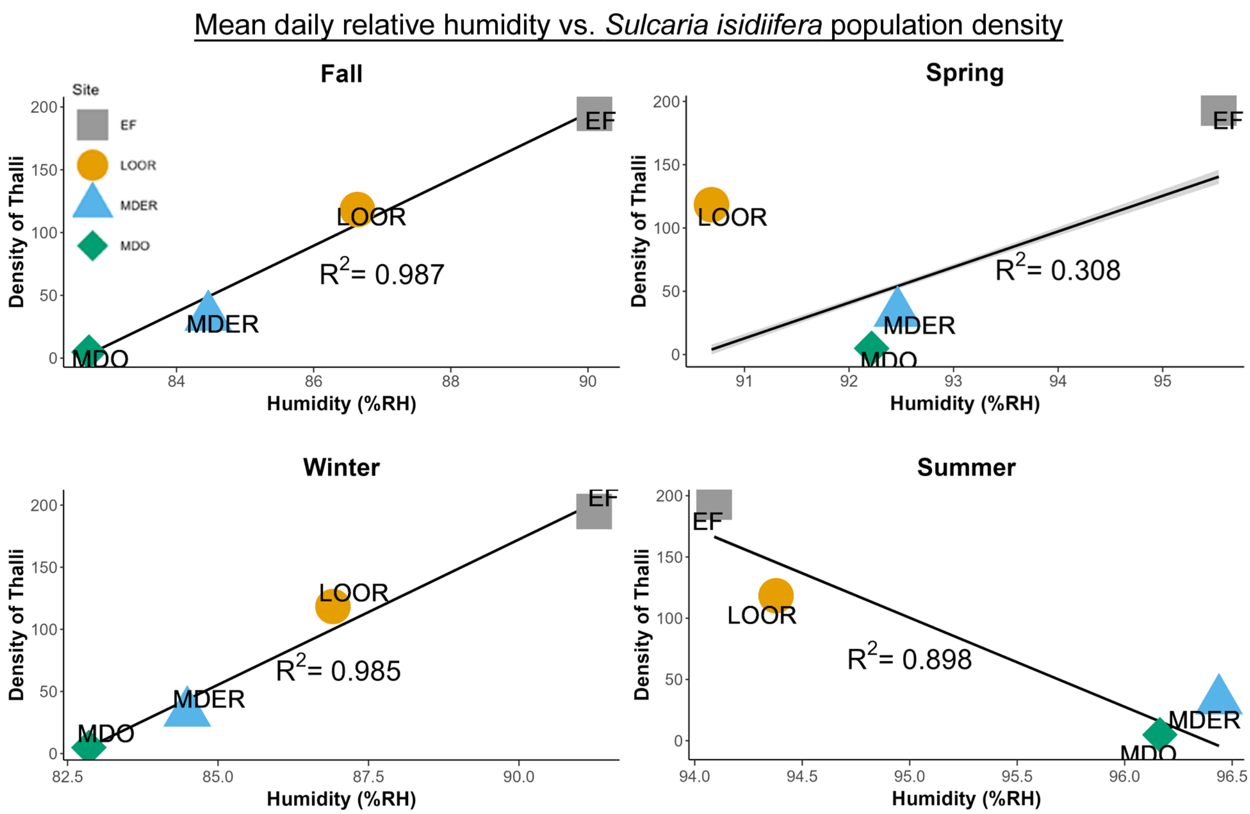


Fig. 7. Population density of *Sulcaria isidiifera* plotted against microhabitat humidity. Sites included Elfin Forest (EF), Los Osos Oaks State Reserve (LOOR), Morro Dunes Ecological Reserve (MDER), and Montaña de Oro State Park (MDO). Lines represent the best linear fit according to ordinary least squares regression between population density and mean daily humidity at each site. Shading around the linear-regression lines represents the 95% CI

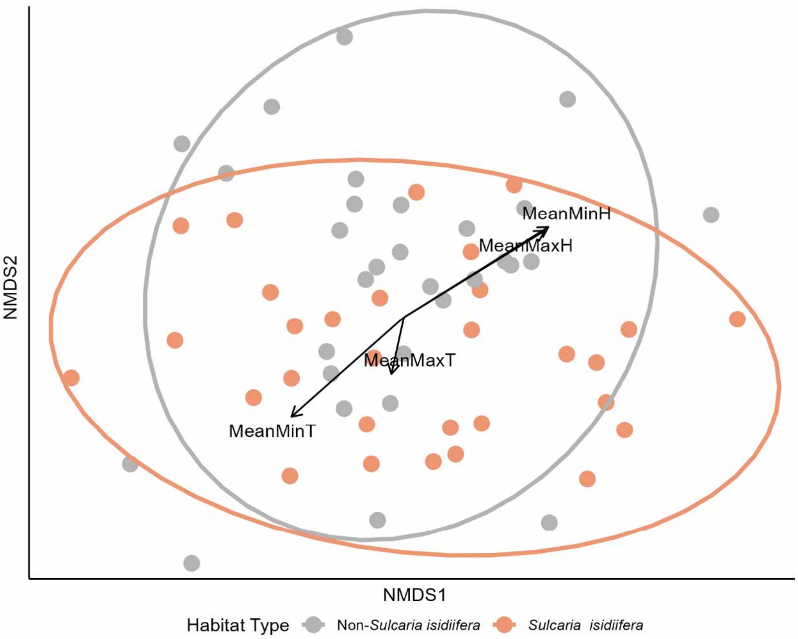


Fig. 8. Nonmetric multidimensional scaling ordination of samples with overlaid vectors for selected environmental variables and ellipses representing 95% CIs of the centroids for both *Sulcaria isidiifera* and non-*S. isidiifera* habitat. Arrows: mean minimum temperature (MeanMinT), mean maximum temperature (MeanMaxT), mean minimum humidity (MeanMinH), and mean maximum humidity (MeanMaxH)

one of which was a control thallus, had lost substantial mass since the end of the initial experiment. In the initial observation after 13.5 mo, $F_v/F_m$ values ranged from 0.639 to 0.782 for translocated thalli, 0.375 to 0.729 for control thalli, and 0.345 to 0.777 for undisturbed thalli (Fig. 9). These values indicate that thallus vitality for transplanted individuals was within a normal range for lichens (Jensen & Kricke 2002). The majority of control thalli and undisturbed thalli also exhibited $F_v/F_m$ values within the normal range for lichens, with the exception of one control thallus and 4 undisturbed thalli. A significant difference in chlorophyll fluorescence was found between the experimental and undisturbed groups of *S. isidiifera* (Welch's 2-sample *t*-test, $t = 3.127$, df = 42.198, p = 0.003). Translocated thalli had significantly higher chlorophyll fluorescence ($\bar{x} = 0.704$, $\sigma = 0.035$; Fig. 9) than undisturbed thalli ($\bar{x} = 0.655$, $\sigma = 0.077$; Fig. 10).

Overall, seasonal values of microhabitat temperature and humidity were very similar when comparing treatment groups, host species, and aspects. However, maximum temperatures were significantly higher on the

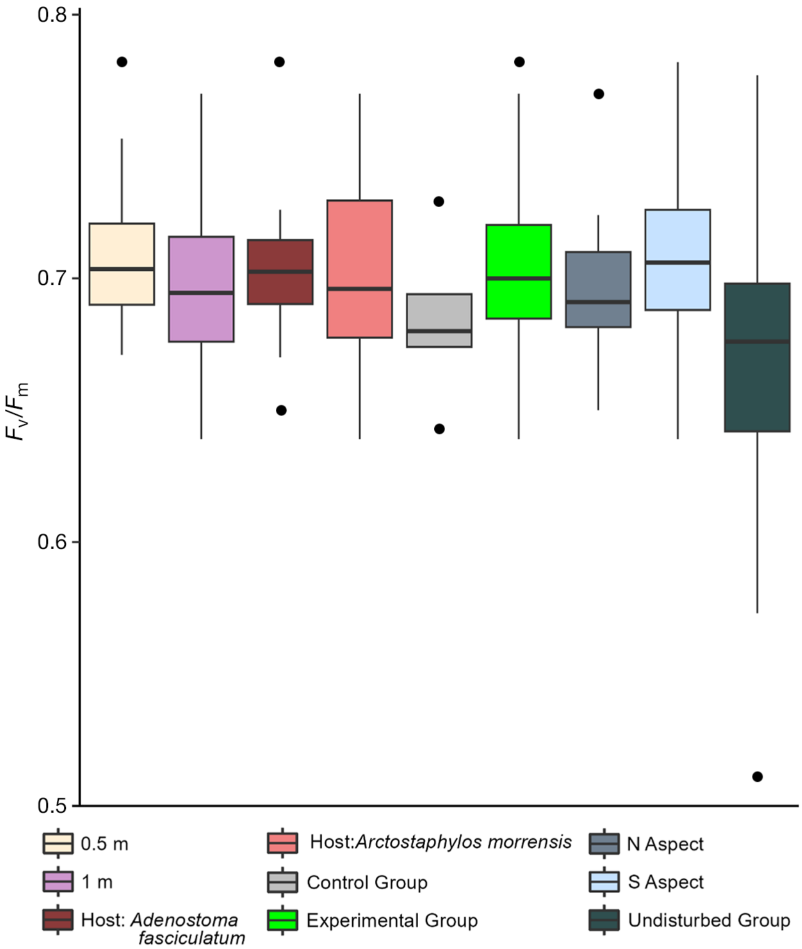


Fig. 9. Chlorophyll fluorescence measurements calculated as $F_v/F_m$. Horizontal lines: median; lower and upper hinges: 25th and 75th percentiles, respectively; upper whiskers: largest observation less than or equal to upper hinges plus 1.5 times the interquartile range; lower whiskers: smallest observation greater than or equal to lower hinges plus 1.5 times the interquartile range; individual points: outliers. $F_v/F_m$ values for all groups fall within the range of normal values for lichens

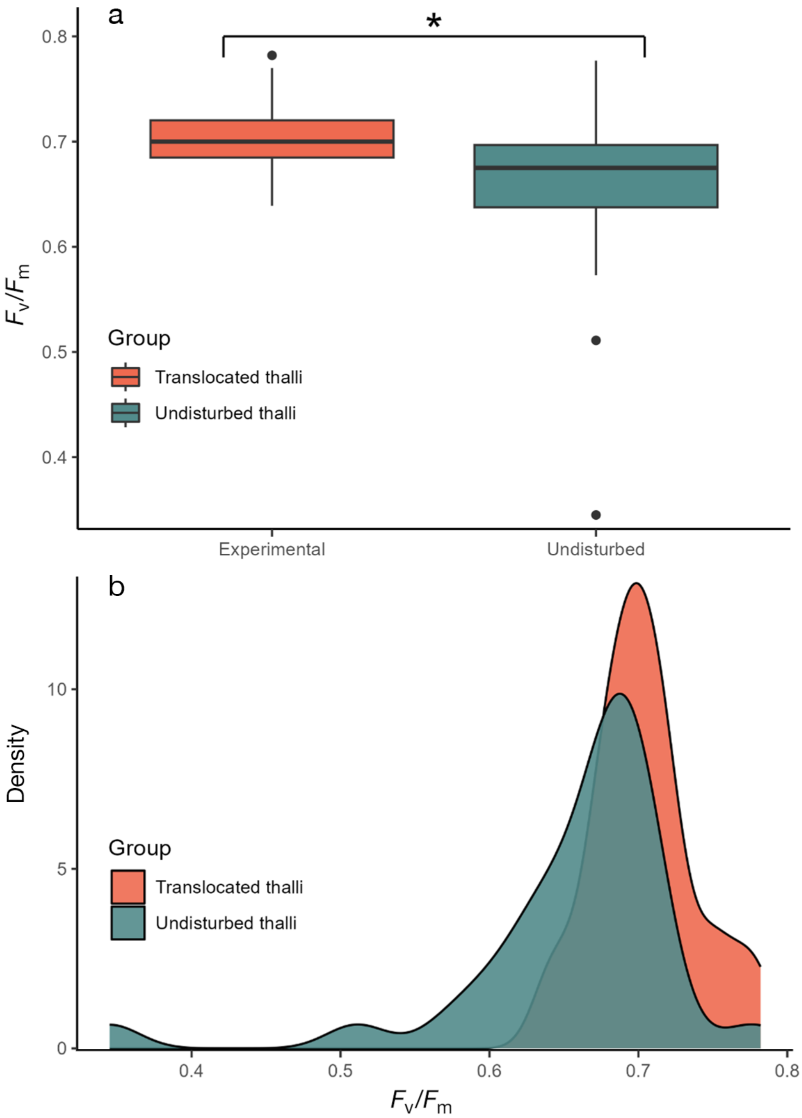


Fig. 10. (a) Boxplots of chlorophyll fluorescence measurements calculated as $F_v/F_m$. Upper whiskers: largest observation ⩽ upper hinge of box + 1.5 × interquartile range; lower whiskers: smallest observation ⩾ lower hinge of box − 1.5 × interquartile range. Upper and lower hinges of boxes: 75 and 25% quantiles, respectively. Middle line in each box: 50% quantile. Individual points: outlying data. Line and star: significant difference between treatment groups ($t_{42.198}$ = 3.127, p = 0.003). However, both group measurements of $F_v/F_m$ fall within the range of healthy lichens. (b) Density plot of chlorophyll fluorescence measurements for experimental and undisturbed *Sulcaria isidiifera* thalli. Distributions are similarly skewed, but undisturbed thalli had significantly lower $F_v/F_m$ measurements ($t_{42.198}$ = 3.127, p = 0.003)

south sides of shrubs (Tukey's HSD, p < 0.001). South sides of shrubs also received higher amounts of PAR in the morning and around midday (Tukey's HSD, p < 0.001; Fig. 11).

Values for the afternoon were not significantly different between aspects. No significant differences in PAR were detected in thalli placed on different host species *A. fasciculatum* and *A. morroensis*. PAR was slightly higher in the morning for control thalli compared to translocated thalli ($F$ = 4.301, df = 2, p = 0.014; Tukey's HSD, p = 0.008). Even with these differences in abiotic conditions, there were no significant differences detected for any of the chlorophyll fluorescence measurements between groups within the translocation trial. The range of $F_v/F_m$ values was also highly similar between the tested groups (Fig. 12).

## 4. DISCUSSION

### 4.1. Overview

*Sulcaria isidiifera* is narrowly restricted to a 24 km$^2$ area on the coast of San Luis Obispo County in several disjunct patches of maritime chaparral habitat. The estimated population size of *S. isidiifera* is 13 841−25 064 individuals growing on 3588−7772 host shrubs. *S. isidiifera* is found primarily on protected lands, and urban development has resulted in the fragmentation of these subpopulations. These results are consistent with the IUCN Red Listing of *S. isidiifera* as Critically Endangered and in need of conservation measures. The methods tested in this study resulted in the successful translocation and survival of 22 out of an initial 24 thalli onto new host shrubs in adjacent suitable habitat. Data gathered to characterize the population and ecology of *S. isidiifera*, along with the methods for translocation that were tested, will support future conservation actions.

*S. isidiifera* surveys found that the species occurs in variable densities within the study area. Some areas of maritime chaparral habitat appeared suitable but did not contain the species. Differences in temperature and RH between sites indicated biologically meaningful differences in microclimate that may explain the observed population density at each site. Lichen thalli with high water content may be more susceptible to heat-induced physiological damage com-

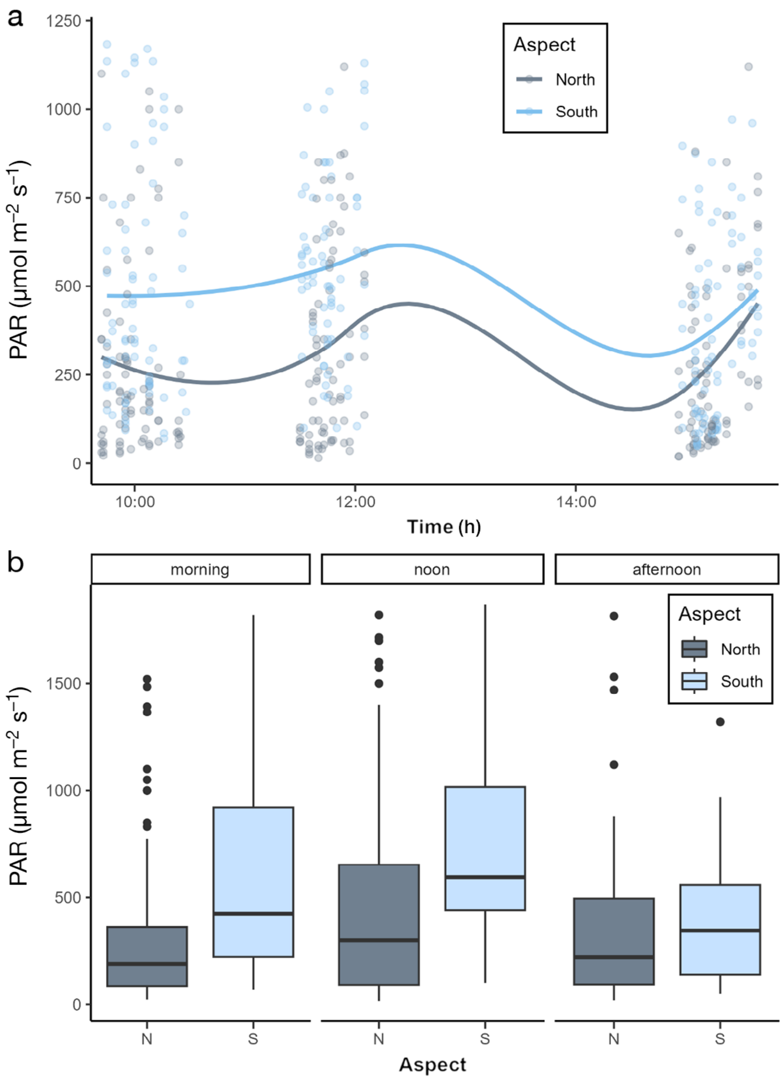


Fig. 11. (a) Photosynthetically active radiation (PAR) displayed as individual points and a smooth curve. (b) Boxplots showing measurements of PAR on translocated *Sulcaria isidiifera* thalli placed on north and south-facing aspects of shrubs. Upper whiskers: largest observation ≤ upper hinge of box +1.5 × interquartile range, lower whiskers: smallest observation ≥ lower hinge of box −1.5 × interquartile range. Upper and lower hinges of boxes: 75 and 25% quantiles, respectively. Middle line in each box: 50% quantile. Individual points: outlying data. Values were measured and compared in the morning, noon, and afternoon

pared to dried thalli, in part because a drier state confers a more stable temperature (Chowaniec et al. 2023). As such, higher humidity may better suit the physiological requirements of *S. isidiifera* propagules, but only during the cooler months of the year. The higher abundance of *S. isidiifera* in areas with higher winter humidity and lower summer humidity may also be due to more successful asexual reproduction under these conditions.

The fact that *S. isidiifera* is found strictly along the central coast of California in an area characterized by heavy fog and mild temperatures further supports its affinity for humidity, whereas the species is absent from the nearby interior areas of central California, where the climate can be dramatically warmer and drier (PRISM Climate Group 2023). This correlation could also signal that the combination of drier droughts and heavier precipitation that are predicted by climate models (Pierce et al. 2018) may either cause a decline of *S. isidiifera* or necessitate migration to more suitable habitat (Glavich et al. 2005, Ellis 2018).

While the effect of temperature on population density was less clear, it is likely that *S. isidiifera* prefers a specific range of temperatures, and that population size will be affected by changing temperatures. Given our limited microclimate data set, exactly how climate change-induced temperature shifts will affect *S. isidiifera* remains unknown. However, in light of this threat, some lichens may need interventions such as assisted migration in order to survive (Borge & Ellis 2024). This is especially true for species with a very limited range and ability to disperse (Allen & Lendemer 2016). The conservation translocation approach tested in this study provides an effective method that can be used as a stopgap measure if *S. isidiifera* faces extinction.

Host preference is also an important factor when predicting the current or future distribution of *S. isidiifera*. Survey results revealed that host preference closely matched vegetation composition, which could indicate that the distribution of *S. isidiifera* among shrub species is somewhat random within the maritime chaparral habitat. Further research into host shrub characteristics is needed to determine the specific factors important to *S. isidiifera* host preference. To determine if there is a preferred host species for *S. isidiifera*, we would need to compare ecological interactions and abiotic factors between shrub species, such as the potential effects of canopy shading, bark texture, and pH, which have been explored in other studies (Ódor et al. 2013, González-Montelongo & Pérez-Vargas 2022). For example,

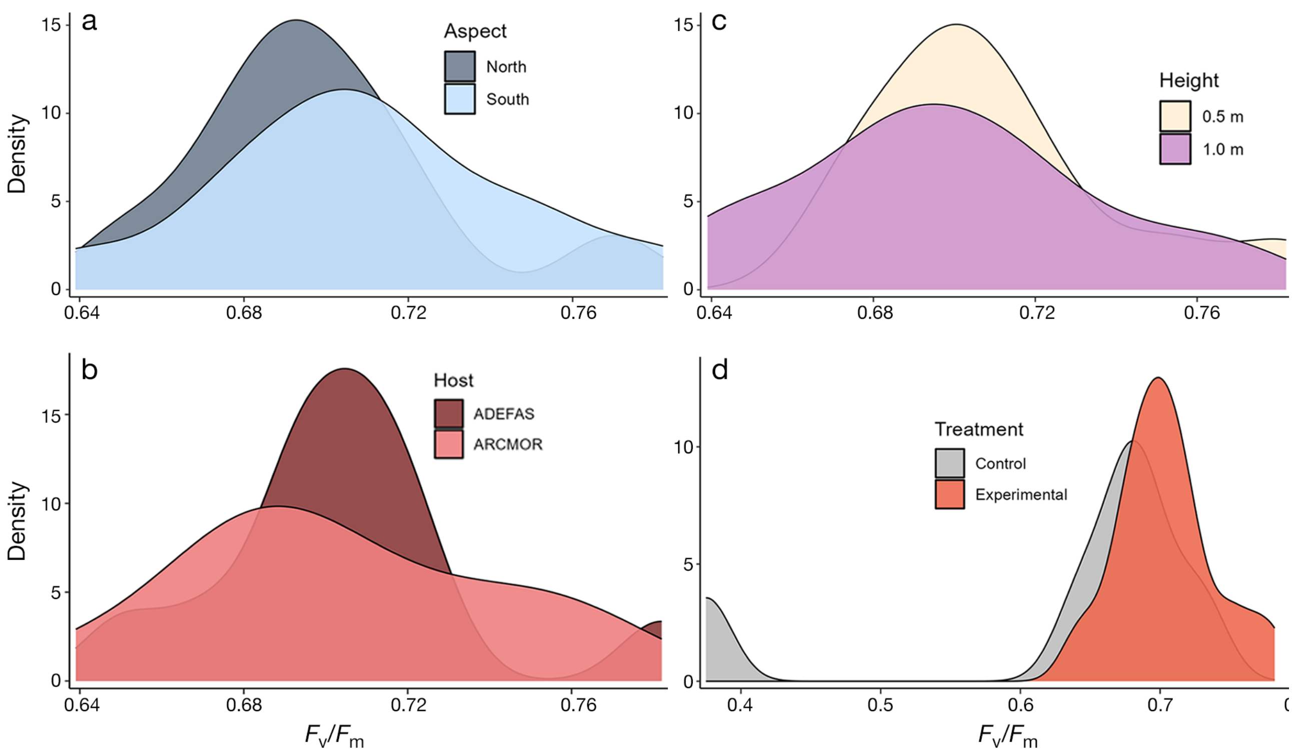


Fig. 12. Density plots of chlorophyll fluorescence ($F_v/F_m$) for all experimental groups, representing (a) aspect distribution, (b) host species distribution, (c) height distribution, and (d) distribution of translocated and undisturbed *Sulcaria isidiifera* thalli. Group means were significantly different from each other

bark texture and stability may strongly affect lichen community structure (Williams & Sillett 2007, Benítez et al. 2019).

Stand age can be an important determinant in vegetation composition and habitat conditions, which in turn will influence lichen composition (Sillett et al. 2000, Miller et al. 2020). This is true for *S. isidiifera*, which has a limited distribution that is likely due in part to its asexual reproductive strategy. Relatively large, asexual propagules, like the isidia of *S. isidiifera*, are not easily spread compared to other propagules such as spores (Sillett et al. 2000). Due to this potentially slow and short-range dispersal of *S. isidiifera*, old-growth stands of maritime chaparral will have a better chance of hosting the species. The vegetation composition in these older stands will differ from younger stands, and could affect the host preferences of *S. isidiifera*. Throughout its habitat, few wildfires have occurred during the period between the late 1890s and 2023 (California Department of Forestry and Fire Protection 2023). While chaparral vegetation is a fire-prone system, wildfire has been mostly eliminated in *S. isidiifera* habitat by modern fire-suppression activities (Odion & Tyler 2002). It is also possible that this type of maritime chaparral habitat is naturally less fire-prone, which might account for the long-lived shrubs that *S. isidiifera* can be found on, as well as the high amount of local endemism (Vasey et al. 2014).

### 4.2. Limitations

While complete population count surveys were exhaustive, there are certainly individuals that were missed in the final population count due to lack of time, inaccessibility of certain locations, and the difficulty of finding *S. isidiifera* visually, due to similar-looking co-occurring species. It is possible that several individuals or clusters of *S. isidiifera* are present in areas that were not included in key survey areas because the vegetation did not meet the expected criteria. Surveys were instead prioritized in areas of more suitable maritime chaparral habitat that were considered more likely to host *S. isidiifera*. Even within key survey areas, some areas were inaccessible due to the density of shrubs. In these particular stands, best efforts were made to check each host shrub while minimizing damage to plants and other organisms, often requiring the use of binoculars.

Additionally, the relatively short time span of the translocation study may not account for the long-term impacts on thalli and the overall success of the tested methods. In addition, only one sensor was used for the measurement of PAR for the translocation experiment, resulting in time gaps of up to 1 h between measurements that occurred while traveling between locations. This led to differences in cloud cover and in the angle of incoming PAR. Best efforts were made to ensure that PAR measurements were taken as close together as possible, and to limit variations in readings. Further long-term data should be collected to better understand the PAR requirements of *S. isidiifera*.

### 4.3. Conservation recommendations

Remaining occupied maritime chaparral habitat for *S. isidiifera* is primarily located on state and locally protected lands. Urbanization of Los Osos and Baywood Park destroyed hundreds of acres of habitat likely occupied by *S. isidiifera*. As many vegetation communities are predicted to shift and undergo changes in diversity by the end of the century (Svenning & Sandel 2013, Feeley et al. 2020, Hill & Field 2021), proactive efforts should be made to maintain the remaining maritime chaparral habitat that *S. isidiifera* occupies through restoration efforts and other conservation actions (Ellis 2018, Riordan et al. 2018). State and local governing agencies that own and/or manage protected lands containing *S. isidiifera* habitat should prepare conservation plans that outline protection and monitoring protocols. If the habitable range of *S. isidiifera* shifts due to climate change, translocation to sites outside of its current range could be warranted (Allen & Lendemer 2016, Borge & Ellis 2024).

The extensive surveys carried out in this study provide population data that can be leveraged by management agencies and landowners to inform future monitoring efforts and mitigate impacts to sensitive habitat. The primary indicator lichen, *Leucodermia leucomelos*, is white and conspicuous, with features that are more easily identifiable to non-specialists, and can guide future survey efforts to target specific areas of conservation concern. This will be especially helpful for identifying potential translocation sites and habitat in areas with lichen flora that are well characterized. Stakeholders should use indicator species and occurrence data to determine if projects will impact *S. isidiifera*, and use translocation if necessary. However, translocation should be the last resort, instead prioritizing habitat preservation; especially since this complements protection of other rare and threatened species, including *Cladonia firma* (Nyl.) Nyl. (California Rare Plant Rank 2B.1), *Sulcaria spiralifera* (California Rare Plant Rank 1B.2), *Arctostaphylos morroensis* (ESA threatened), and *Helminthoglypta walkeriana* (ESA threatened).

Data gathered from the translocation study should be used by land managers to guide and further develop methods to translocate individuals and potentially small, disjunct populations of *S. isidiifera* that are threatened by disturbance. Continued monitoring of translocated thalli will be necessary to assess the long-term impacts of translocation, since the longevity of translocated individuals is not yet known. Nonetheless, *S. isidiifera* appears to be amenable to translocation; it does not have the same level of interactions or disturbance associated with moving many plants and animals, and may be considered a low-risk and low-cost candidate for translocation (Berger-Tal et al. 2020, Zimmer et al. 2019). In areas where disturbances are planned, efforts should be made to mitigate the loss of *S. isidiifera* by implementing pre-project surveys carried out by trained biologists. Translocation could also, with caution, be used to populate unoccupied habitat within the species' range.

Translocation sites should be selected based on their vegetation composition, microclimate, ease of access, and level of protection. Maritime chaparral is the preferred habitat for *S. isidiifera*, and ideal host shrubs include *Adenostoma fasciculatum*, *A. morroensis*, and *Ceanothus cuneatus*. To prevent further damage to the population, hosts should be selected that are close to trails or roads, but also that are not directly within frequently used pathways. Ideal host shrubs would be located near other *S. isidiifera*-occupied shrubs, but would not already host *S. isidiifera* individuals, which should minimize disturbance to other thalli. Ideal positions on hosts are the north sides of shrubs and on sheltered branches with limited direct exposure to wind and rain. Placement on bare branches is preferred to prevent damaging other epiphytes. An additional factor that should be considered is genetic diversity. Zoller et al. (1999) suggested that placing translocated individuals near smaller, more isolated existing subpopulations might help improve genetic diversity, and thus also improve the chance of survival for those subpopulations. Despite *S. isidiifera* only being known to reproduce asexually, it would be a good practice to follow this suggestion when feasible. This practice would help enhance smaller population sizes by the addition of new individuals, increasing the chance of survival from catastrophic events such as wildfire, which could potentially destroy large portions of populations. Such disturbances are especially of concern for species with very small ranges like *S. isidiifera*.

During translocation, whole thalli, along with some substrate, should be collected. This will allow epoxy to be applied to the underside of the substrate without touching the thallus. Nylon monofilament fishing line can be used to further secure the thalli while the epoxy cures. The line should be removed after curing to prevent strangling of the host branch.

Translocation would ideally occur during the wet season, which in California is between November and April. This strategy is recommended for most lichen translocations because wet conditions have been found to be important in thallus development (Smith 2014), whereas dry conditions following translocation can negatively impact success rates (Hazell & Gustafsson 1999).

Within the first week of translocation, thalli should be checked to ensure they are still secure on the new host, and any issues should be addressed immediately. For the remainder of the wet season, monthly checks, as well as after storms that could result in thallus detachment, are recommended. During these monitoring events, data gathered should include visual health inspections, presence of new attachments, overall growth, and other environmental changes such as fallen trees or broken host plant branches. Given that *S. isidiifera* branches were observed to form attachments to their new hosts, it is a good indicator of the successful establishment of translocated thalli, and could be used as an indication that monitoring frequency can be reduced (Anstett et al. 2014). To further characterize abiotic conditions, microclimate sensors placed near thalli could be used to monitor temperature and humidity. These data can be aggregated over time to detect long-term trends that might arise due to climate change. Changing conditions may necessitate the further translocation of *S. isidiifera* and other sensitive species to refugia with more suitable microhabitats. The relatively low cost and apparent low risk associated with translocating *S. isidiifera* will allow for the implementation of this mitigation strategy.

Given the current IUCN criteria and our population count data, *S. isidiifera* should maintain its current status as Critically Endangered B2ab(i,ii,iii,iv,v). The values for AOO and EOO, along with historical and ongoing threats, support this recommendation (IUCN Standards and Petitions Committee 2022). Continued threats from development and a previously noted decline in mature individuals (McMullin et al. 2019) both contribute to this recommended status. Under these criteria, *S. isidiifera* should also be listed under the ESA, where qualifying factors include the 'present or threatened destruction, modification, or curtailment of its habitat or range; inadequacy of existing regulatory mechanisms; or other natural or manmade factors affecting its continued existence' (Federal ESA, 16 U.S.C. § 4). While the California Endangered Species Act (CESA) does not currently support the listing of lichens, efforts should also be made to broaden the scope of CESA to include more underrepresented taxa. This will open opportunities for legal protection, and increase awareness of the important ecosystem roles of lichens and other traditionally overlooked organisms.

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