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ORIGINAL PAPER

Historical resurvey indicates no decline in Argentine ant site occupancy in coastal southern California

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Abstract Predicting changes in the abundance and distribution of introduced species over time is difficult, but clues regarding the underlying causes of these changes may come from long-term surveys. Resurveys conducted over large spatial scales, for example, can be used to discriminate between site-specific causes of decline and those that act at the population level. Here we used regional resurvey data to address changes in Argentine ant site occupancy in urban, agricultural, and natural environments in coastal southern California. We resurveyed 145 locations originally sampled 12–14 years ago and observed a slight decrease in Argentine ant site occupation, from 85 to 79% across all sites. At the majority of sites where apparent absences were recorded, however, the Argentine ant had merely retreated outside of the proscribed sampling area (a 25-m radius circle) and was still present within 80 m, on average, of the original sampling point. This finding thus suggests that the apparent absences observed most likely reflect contractions of the area occupied by polydomous supercolonies, possibly in response to local-scale changes in environmental conditions, as opposed to processes acting at larger spatial scales. We also conducted back-to-back annual resurveys (in 2018 and 2019) of all urban sampling points (n = 95) to quantify annual turnover in site occupancy. These resurveys revealed 2.4% site turnover with 97% (92/95) sites being classified as either presences (n = 85) or absences (n = 7) in both years. Our results support the findings of resurveys conducted in northern California, where Argentine ant distributions have slowly expanded over decadal time scales. Historical resurveys can provide insights into why populations of introduced species change over time and should incorporate an appreciation of how invader traits affect detectability.

Keywords California · Formicidae · Historical resurvey · Introduced species · Invasion · *Linepithema humile* · Urbanization

Introduction

Long-term studies of species introductions are rare (Strayer 2012). Although impacts caused by biological invasions can persist over decadal time scales without evidence of change (Sharpe et al. 2017; Doody et al. 2017; Menke et al. 2018), populations of introduced species can also grow or shrink over time with commensurate shifts in invasion impacts (Strayer

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et al. 2006; Strayer 2012). The causes of such changes remain somewhat conjectural (Simberloff and Gibbons 2004; Strayer 2012), but clues regarding the underlying mechanisms of long-term changes in the populations of introduced species may come from historical resurveys that document spatial or temporal patterns of shifts in population size or distribution.

Introduced ant populations can decline in abundance and contract in distribution with increasing time since invasion (Cooling and Hoffmann 2015; Lester and Gruber 2016; Tartally et al. 2016), but the generality of this phenomenon is uncertain because of the scarcity of data sets that span sufficient lengths of time to document losses in abundance or distribution (Holway et al. 2002) and because of the geographically restricted focus of most published studies that document invader declines (Heller et al. 2008; Morrison 2002). Long-term and large-scale studies are thus needed to clarify how and why the ecological impacts and distribution of introduced ant species change over time (Menke et al. 2018). Regional-scale resurveys are of value in that they can be used to discriminate between site-specific causes of decline and larger-scale, population-level changes. Resurveys that span multiple years can be used to separate intra-annual variation in abundance (e.g., changes in colony size at different points in the colony cycle) from long-term, directional changes in population size.

In this study we resurveyed 145 locations that were originally sampled 12–14 years ago in coastal southern California (Backlin et al. 2005; Menke et al. 2009) with the general goal of determining if Argentine ant site occupancy has declined during this time. Our sampling points encompassed a range of environments, but we focused on urbanized areas for several reasons. The Argentine ant is an urban pest (Knight and Rust 1990; Cooling et al. 2011; Greenberg et al. 2015), but few published studies have evaluated whether or not urban areas support temporally stable infestations. In Bermuda, the Argentine ant has persisted at a variety of locations, including urbanized areas, over an approximately 60-year period (summarized in Wetterer 2017). In New Zealand, however, Cooling et al. (2011) documented Argentine ant declines over a 12-year period in urban areas on both the North and South Islands. Moreover, Menke et al. (2018) found that urban environments in northern California were potentially overrepresented, relative to riparian woodland environments, among sites where apparent losses were recorded. These latter studies suggest that Argentine ant infestations in urban areas could be particularly susceptible to declines, but the small number of studies available leaves this question open. The motivation for our study is to clarify the longevity of Argentine ant infestations with the larger goal of understanding where and ultimately why changes in distribution and abundance occur.

Methods

Our resurveys are based on two studies (Backlin et al. 2005, Menke et al. 2009) that aimed to document the distribution of the Argentine ant in different parts of coastal southern California. In these original surveys the Argentine ant was present at 85% (123/145) of sampling points (Table 1). We used GPS coordinates from the original studies to locate all sampling points in 2018 ("Appendix"). We corroborated GPS coordinates with additional data, which allowed us to return to the original point of sampling with a high degree of certainty. From the Backlin et al. (2005) survey, we revisited sampling points (n = 20) in natural environments on Santa Catalina Island, Los Angeles Co., CA ("Appendix"). Corroboration of the location of these sampling points was possible because of material (e.g., drift fences and buckets) left behind from the original survey (Backlin et al. 2005), which was designed for sampling reptiles and amphibians in a representative sample of island habitats. From Menke et al. (2009), we revisited 125 sampling points in urban (n = 95), agricultural (n = 16), and natural (n = 14) environments distributed across the coastal portions of San Diego Co., CA (Fig. 1, "Appendix"). Although Menke et al. (2009) included sampling points from a stratified random sample of habitats throughout San Diego Co. and Imperial Co., we used only a subset of these points (all within 45 km of the Pacific Ocean) in the present study given that many of the points sampled in the original study were in environments (e.g., deserts, mountains) known to be abiotically unsuitable for the Argentine ant (Menke et al. 2007, 2009). An additional number of agricultural and natural points from Menke et al. (2009) that were near the coast were also not included in our 2018 resurvey because of issues relating to access or (in a small number of cases) because they had since

Table 1 Change in the proportion of sites occupied by the Argentine ant between surveys conducted in the mid-2000s and resurveys conducted in 2018 in urban, agricultural, and undeveloped environments in coastal southern California

Environment	Date of original survey	Proportion occupied in original survey	Proportion occupied in 2018 resurvey	Proportional change
Urban	2006*	0.98 (93/95)[a]	0.92 (87/95)[a]	− 0.06
Agricultural	2006*	0.56 (9/16)[b]	0.63 (10/16)[b]	+ 0.07
Natural	2006*	0.71 (10/14)[b]	0.64 (9/14)[b]	− 0.07
Natural	2002–2004**	0.55 (11/20)[b]	0.45 (9/20)[b]	− 0.10

Dates of original surveys are from *Menke et al. (2009) and **Backlin et al. (2005). Different superscripts correspond to statistically different proportions (Fisher Exact Tests, $P < 0.05$) of sites occupied by the Argentine ant in the three different types of environments (original survey and resurvey considered separately)

changed from one land use type to another (e.g., from agricultural to urban). In urban locations, each sampling point was associated in the original study with a street address, and the sampling point was defined as the midpoint of the property lot facing the street. For agricultural and natural sites, GPS coordinates and details from field notes were both used to definitively locate sampling points.

The environments originally surveyed in Backlin et al. (2005) and Menke et al. (2009) differed in terms of their degree of human modification ("Appendix"). Sampling points in urban environments were primarily in residential neighborhoods that supported ornamental vegetation (i.e., mostly non-native) that was typically irrigated. A few urban sampling points were in lightly industrialized locations, but irrigated ornamental vegetation was a common element of all urban points. Sampling points in agricultural environments were in areas supporting irrigated orchards (e.g., mostly citrus or avocado) or annual crops but also a mixture of native and non-native vegetation. Sampling points in natural environments from both Backlin et al. (2005) and Menke et al. (2009) were in a mixture of grassland, scrub and woodland habitats. Perennial vegetation surrounding sampling points in natural environments was largely to entirely native.

Although the methods and level of effort used in Backlin et al. (2005) and Menke et al. (2009) differed, the spatial scale of the sampling was comparable, and both sets of methods provide an unambiguous record of Argentine ant presence/absence. Backlin et al. (2005) relied on pitfall traps to sample ants. Around each sampling point, they deployed five pitfall traps (50-ml centrifuge tubes) in the configuration of a five on a die (with 20 m on a side and with the center trap placed at the sampling point). Traps were left in the ground for 10 days, twice a year on six occasions between 2002 and 2004 (Backlin et al. 2005). In Menke et al. (2009) bait surveys and visual searches were used to detect ants within 25 m of each sampling point. At each point, surveys lasted a maximum of 45 min; if the Argentine ant was detected prior to 45 min, then the survey ended immediately after detection. Surveys took place in the spring and summer of 2006 and were conducted by the first author.

In the 2018 resurvey, we primarily used visual surveys to determine the presence or absence of the Argentine ant. We visually searched for ants by examining bare ground, vegetation (especially tree trunks), and under stones and logs. This approach is an effective means of detection for this species (Menke et al. 2018), especially in environments supporting open vegetation, which characterized nearly all of our sites. Visual surveys were conducted in May under mild weather conditions in which Argentine ant activity was high. At each point, surveys lasted 45 min or until the Argentine ant was detected. We restricted sampling to an area within 25 m of each original sampling point, and hereafter use the term 'site' to refer to the area searched within 25 m of each sampling point. Changes in site occupancy were analyzed using Fisher's exact test.

For the sampling points (n = 95) in urban environments (all from Menke et al. 2009), we conducted two different types of resampling. First, at sites where the Argentine ant was detected in 2006 but not in 2018, we revisited these sites on two additional occasions in 2018 (once each in May and November). Documentation of apparent absences represents a general

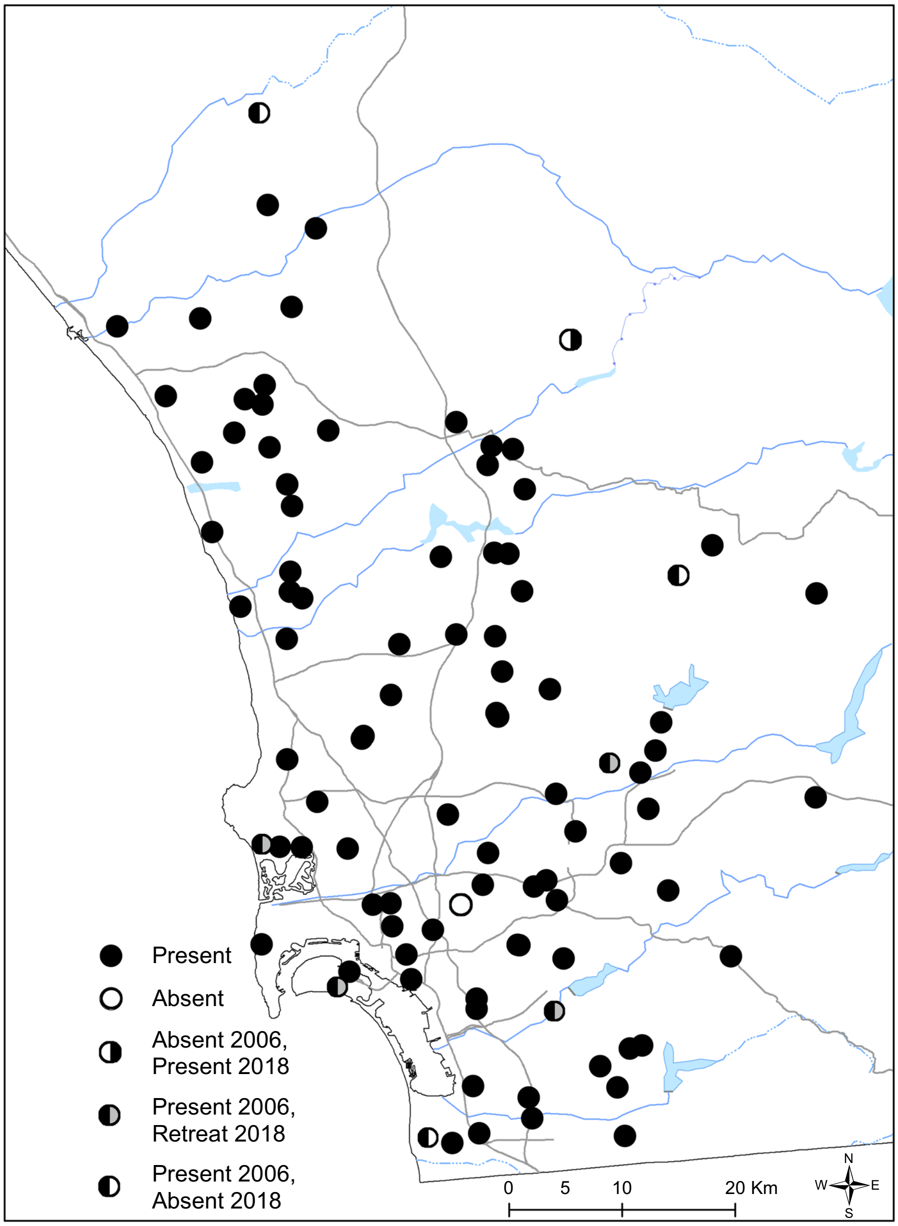

Fig. 1 Map of western San Diego Co., CA indicating major roads, watercourses, and the location of 95 urban points sampled for Argentine ant presence/ absence in 2006 (Menke et al. 2007) and 2018 (present study). Symbols indicate the following: solid circle, Argentine ants always present; open circles, Argentine ants never present; half open/half solid, sites invaded between 2006 and 2018; half solid/half shaded, sites in which Argentine ants were present in 2006 but absent within the 25-m sampling radius in 2018, but found within 100-m of the point; half solid/half open, sites in which Argentine ants were present in 2006 but apparently absent in 2018

challenge in historical resurveys, and repeated, site-level sampling serves as an objective and recommended method to cope with this challenge (Tingley and Beissinger 2009). During May and November revisits, we also expanded the radius of sampling from 25 to 200 m away from sampling points in attempt to discriminate between sites where the Argentine ant was actually absent and sites where this species had locally retreated outside of the area defined by the 25-m radius of sampling. Second, to document site-level, annual turnover in Argentine ant presence/ absence, all urban sampling points (n = 95) in May 2019 were resurveyed using identical methods to those used in the 2018 resurvey. We estimated annual site turnover as in Morrison (1998), where the sum of the sites gaining and losing the Argentine ant between 2018 and 2019 is divided by the sum of the sites where this species was present in 2018 and 2019. In the 2019 resurvey, we also revisited all sites where local retreats were observed in 2018 and 2019 and measured the distance between the original sampling point and the nearest detected Argentine ant infestation (within

200 m) in July 2019. Given that we were not able to search all portions of the area surrounding each sampling point (e.g., backyards of private residences), these measures should be considered maximum distance estimates.

Results

The 2018 resurvey revealed slight decreases in the proportion of sites occupied by the Argentine ant in urban and natural environments and slight increases in the proportion of sites occupied by the Argentine ant in agricultural environments (Table 1, Fig. 1). The Argentine ant was present at a higher proportion of sites in urban environments compared to sites in natural and agricultural environments both in the original surveys and in the 2018 resurvey (Table 1). Of the seven urban sites at which the Argentine ant was detected in 2006 but not in 2018, we were able to find Argentine ant workers within 100 m of the original sampling point at four sites in 2018, indicating a local retreat in distribution rather than an extirpation (Fig. 1). An additional example of a local retreat was observed in 2018 on Santa Catalina Island. At many of the sampling points where we recorded local-scale retreats, we observed established colonies of native ants (e.g., *Aphaenogaster patruelis* (on Santa Catalina Island), and *Tapinoma sessile* (at urban sites)).

The 2018 and 2019 resurveys of urban sites yielded highly consistent findings with 95% (92/95) of sites being classified as either presences (n = 85) or apparent absences (n = 7) in both years. We estimated turnover to be 2.4% with two sites losing and one site gaining the Argentine ant over this one-year sampling interval. Changes in status at these three sites involved local movements of the Argentine ant in and out of the 25-m radius sampling area. As in 2018, at most (6/8) of the sites that were recorded as apparent absences in 2019, we were able to find the Argentine ant outside of the 25-m radius sampling area with an estimated retreat distance of 79.5 $\pm$ 11.4 m (mean $\pm$ SE). The ubiquity of the Argentine ant in urban environments is underscored by the fact that this species went undetected from only a single sampling point when the 2006 and 2018 surveys are pooled together (Fig. 1). At this one sampling point, the 2018/2019 resurveys revealed the presence of *Pheidole megacephala* (specimen vouchered with the California Department of Food and Agriculture), a geographically widespread invader, which colonized the area surrounding this point at some time since the original 2006 survey.

Discussion

The findings of this study are broadly consistent with the results of resurveys conducted in northern California (Holway 1995; Menke et al. 2018) and Bermuda (Wetterer 2017), where Argentine ant distributions have changed relatively little over decadal time scales. In the present study, site occupation by the Argentine ant slightly decreased from 85 to 79% across all sites over a time span of 12–14 years. At the majority of urban sites where we recorded apparent absences, however, the Argentine ant was found within about 80 m, on average, of the original sampling point, suggesting that these observed absences most likely reflect local-scale changes in environmental conditions as opposed to processes acting at larger spatial scales. Identical resurveys conducted in 2018 and 2019 at urban sites revealed a low amount of site turnover, which in all cases resulted from local colony movement in and out of the sampling area.

The high proportion of urban sampling points at which the Argentine ant was present in this study is consistent with the status of this species as a prominent urban pest in coastal southern California (Knight and Rust 1990; Greenberg et al. 2015). Moreover, proximity to urban areas was the strongest predictor of Argentine ant presence in a regional-scale analysis of the occurrence of this species in southern California (Menke et al. 2007). It is noteworthy that despite the pest control industry's long-standing efforts to manage the Argentine ant in California through the use of pesticides, this species was consistently present (i.e., across survey periods) at over 90% of urban sites in this study (Table 1). The lower occupancy of agricultural and natural environments, compared to urban environments, presumably reflects the Argentine ant's inherent dispersal limitations as well as its physiological intolerance of dry conditions (Menke and Holway 2006, 2007; Menke et al. 2007; Schilman et al. 2007).

At both urban and natural sites, local-scale retreats by the Argentine ant were evident over the time frame of this study. Observations of the Argentine ant at these sites between 2018 and 2019 suggest that local-scale retreats represent contractions of the area occupied by polydomous supercolonies. Although we cannot identify a specific cause of these retreats based on the evidence at hand, similar phenomena have been observed in both multi-year observational studies (Holway 1998; Sanders et al. 2001) and shorter-term experimental studies (Menke and Holway 2006), and dry conditions represent a plausible explanation for the retreats observed in this study. Over a 6-month period, Menke and Holway (2006), for example, used irrigation to induce the local spread of the Argentine ant; shutting off the water caused this species to retreat back to the nesting locations observed at the start of the experiment (Menke and Holway 2006). Reductions in residential water use in San Diego Co. over the past decade thus represent a possible mechanism for the retreats observed in this resurvey given the results of Menke and Holway (2006) and given that urban areas in this region are currently a heterogeneous patchwork of irrigated and largely non-irrigated (xeriscaped) urban landscaping at the scale of individual, private residences. It also seems likely that some of the observed retreats may have been caused by pesticide treatments around private residences (Greenberg et al. 2015).

Given the known ecological effects of ant invasions (Holway et al. 2002; Lach et al. 2010; Cameron et al. 2016) and the declines documented for some introduced ant populations (Lester and Gruber 2016), historical resurveys have provided and will continue to provide an invaluable means by which to examine temporal changes in the distribution and abundance of introduced ant species as well as changes in the impacts associated with their invasions. The value of such resurveys, however, can be enhanced by tailoring survey protocols to particular traits of the focal invader. Colony structure, point in the colony cycle, seasonal activity patterns, and foraging behavior all influence detectability. Our sampling window (i.e., a 25-m radius circular area), for example, was too small to take into account local-scale movements that occurred even over the time frame of back-to-back annual surveys. Given the seminomadic behavior of the Argentine ant (Markin 1970), the local retreats observed in our resurvey may not reflect actual declines as much as colony-level movements, possibly in response to changing environmental conditions. Experiments demonstrate the capacity for this species to relocate in response to abiotic stress and changes in resource availability (Holway and Case 2000; Menke and Holway 2006; Heller and Gordon 2006). Moreover, given the well-known difficulties of determining that a species is absent from a location as opposed to being present but not detected (Tingley and Beissinger 2009), resurveys that incorporate repeated sampling (both within and among years) can incorporate detection probability into assessments of whether or not a species is actually absent from a site. Although our back-to-back annual resurveys yielded similar findings, the 2.4% turnover that we did observe again suggests the value of widening the spatial scale of sampling given that inter-annual changes in site occupancy seem to have resulted more from local colony-level movement rather than from extinction–colonization dynamics. It seems likely that site turnover could be higher in environments that are marginal (i.e., relative to irrigated urban areas) from the Argentine ant's perspective.

Although the present study focused only on the distribution of the Argentine ant, the future distribution of this species seems likely to be influenced by the establishment and spread of other species of behaviorally dominant, non-native ants. The unexpected presence of *P. megacephala* at one of our urban sampling points and the widespread occurrence of the red imported fire ant (*Solenopsis invicta*) elsewhere in this region (Kabashima et al. 2007; Greenberg et al. 2015) hint at the potential for ant assemblages in urban areas to shift over time as other invaders colonize and spread in this region. Documenting assemblage-level changes will require community-level sampling procedures beyond those employed in the present study where documenting Argentine ant site occupancy was the main goal. Community-level sampling might be interesting to conduct in light of the suite of non-native ant species currently established in this region.

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Appendix 1: Details and locations of sites resurveyed in this study

Site no.	Environment	Latitude	Longitude	Original	2018 resurvey	2019 resurvey	Original study
5	Urban	32.62678621	116.9818485	Present	Present	Present	Menke et al. (2009)
23	Urban	33.1193665	− 117.244925	Present	Present	Present	Menke et al. (2009)
35	Urban	32.61001047	116.9679318	Present	Present	Present	Menke et al. (2009)
61	Urban	32.64322403	116.9483704	Present	Present	Present	Menke et al. (2009)
274	Urban	32.82708903	117.1029112	Present	Present	Present	Menke et al. (2009)
275	Urban	33.08590861	117.0416633	Present	Present	Present	Menke et al. (2009)
276	Urban	32.57104131	− 116.9619	Present	Present	Present	Menke et al. (2009)
277	Urban	32.75626503	117.1484449	Present	Present	Present	Menke et al. (2009)
278	Urban	32.61089361	117.0829794	Present	Present	Present	Menke et al. (2009)
279	Urban	32.569722	117.1174795	Present	Absent	Absent	Menke et al. (2009)
280	Urban	32.76954664	− 117.034407	Present	Present	Present	Menke et al. (2009)
281	Urban	32.97026346	117.0962053	Present	Present	Present	Menke et al. (2009)
282	Urban	33.03440856	117.0547898	Present	Present	Present	Menke et al. (2009)
283	Urban	32.7663912	116.9275232	Present	Present	Present	Menke et al. (2009)
284	Urban	33.0351485	117.0660757	Present	Present	Present	Menke et al. (2009)
285	Urban	32.701944	− 117.181111	Present	Present	Present	Menke et al. (2009)
286	Urban	32.87777578	− 116.937719	Present	Present	Present	Menke et al. (2009)
287	Urban	32.90484147	117.0628772	Present	Present	Present	Menke et al. (2009)
288	Urban	32.735137	− 117.115	Present	Present	Present	Menke et al. (2009)
289	Urban	32.99894524	117.2187314	Present	Present	Present	Menke et al. (2009)
290	Urban	32.57344561	117.0781294	Present	Present	Present	Menke et al. (2009)
291	Urban	32.83139	− 116.9433	Present	Present	Present	Menke et al. (2009)
293	Urban	32.81361	− 117.0014	Present	Present	Present	Menke et al. (2009)
294	Urban	32.78835531	116.9653035	Present	Present	Present	Menke et al. (2009)
297	Urban	32.72329124	117.0474432	Present	Present	Present	Menke et al. (2009)
298	Urban	33.22191828	117.3001436	Present	Present	Present	Menke et al. (2009)
299	Urban	32.72286922	117.0460406	Present	Present	Present	Menke et al. (2009)
300	Urban	32.87092199	117.2308378	Present	Present	Present	Menke et al. (2009)
301	Urban	33.13920809	− 117.096345	Present	Present	Present	Menke et al. (2009)
302	Urban	32.94086988	117.0597715	Present	Present	Present	Menke et al. (2009)
303	Urban	32.88721885	117.1714977	Present	Present	Present	Menke et al. (2009)
306	Urban	32.92684342	117.0218255	Present	Present	Present	Menke et al. (2009)
307	Urban	32.99255736	117.2681443	Present	Present	Absent	Menke et al. (2009)
308	Urban	32.79632195	117.0707732	Present	Present	Present	Menke et al. (2009)
309	Urban	33.00451625	117.2285746	Present	Present	Present	Menke et al. (2009)
310	Urban	32.71559468	117.1360708	Present	Present	Absent	Menke et al. (2009)
311	Urban	33.02031645	117.2284821	Present	Present	Present	Menke et al. (2009)
312	Urban	33.31222	− 117.2461	Present	Present	Present	Menke et al. (2009)
313	Urban	33.15760595	− 117.264432	Present	Present	Present	Menke et al. (2009)
314	Urban	32.86028	− 116.9497	Present	Present	Present	Menke et al. (2009)
315	Urban	32.60177137	117.0386005	Present	Present	Present	Menke et al. (2009)
316	Urban	32.86812654	116.9758407	Present	Absent	Absent	Menke et al. (2009)
317	Urban	33.13262503	117.1981462	Present	Present	Present	Menke et al. (2009)
318	Urban	32.88943233	117.1700743	Present	Present	Present	Menke et al. (2009)
320	Urban	33.04109379	116.8924022	Present	Present	Present	Menke et al. (2009)
321	Urban	33.11782386	117.0512914	Present	Present	Present	Menke et al. (2009)

continued

Site no.	Environment	Latitude	Longitude	Original	2018 resurvey	2019 resurvey	Original study
322	Urban	33.10710196	117.2986111	Present	Present	Present	Menke et al. (2009)
324	Urban	33.385556	− 117.253056	Present	Absent	Absent	Menke et al. (2009)
325	Urban	32.96889231	− 117.065189	Present	Present	Present	Menke et al. (2009)
327	Urban	33.08961869	117.2309009	Present	Present	Present	Menke et al. (2009)
328	Urban	33.05192739	117.2904147	Present	Present	Present	Menke et al. (2009)
329	Urban	32.72370643	117.2513005	Present	Present	Present	Menke et al. (2009)
330	Urban	33.21556	− 117.3661	Present	Present	Present	Menke et al. (2009)
332	Urban	33.20478756	117.0067354	Absent	Present	Present	Menke et al. (2009)
333	Urban	33.16879195	117.2488191	Present	Present	Present	Menke et al. (2009)
334	Urban	33.00289749	116.8095432	Present	Present	Present	Menke et al. (2009)
335	Urban	32.80098882	− 117.2192	Present	Present	Present	Menke et al. (2009)
336	Urban	32.75878858	117.0162106	Present	Present	Present	Menke et al. (2009)
337	Urban	32.75522773	117.0921921	Absent	Absent	Absent	Menke et al. (2009)
338	Urban	32.77124416	117.0751897	Present	Present	Present	Menke et al. (2009)
339	Urban	32.8000151	117.1828142	Present	Present	Present	Menke et al. (2009)
340	Urban	32.840556	− 116.810278	Present	Present	Present	Menke et al. (2009)
341	Urban	33.15979491	117.3273316	Present	Present	Present	Menke et al. (2009)
342	Urban	32.96266632	117.1413883	Present	Present	Present	Menke et al. (2009)
344	Urban	33.13083	− 117.2728	Present	Present	Present	Menke et al. (2009)
345	Urban	32.71231296	117.0109828	Present	Present	Present	Menke et al. (2009)
346	Urban	32.565556	− 117.099444	Present	Present	Present	Menke et al. (2009)
347	Urban	32.64091693	116.9582234	Present	Present	Present	Menke et al. (2009)
349	Urban	32.69588952	117.1319922	Present	Present	Present	Menke et al. (2009)
350	Urban	32.66963603	117.0183732	Present	Absent	Absent	Menke et al. (2009)
351	Urban	33.1534145	117.2503189	Present	Present	Present	Menke et al. (2009)
352	Urban	32.90021026	116.9332782	Present	Present	Present	Menke et al. (2009)
353	Urban	32.75520281	117.1625171	Present	Present	Present	Menke et al. (2009)
354	Urban	33.0725615	117.2267639	Present	Present	Present	Menke et al. (2009)
355	Urban	32.80117696	117.2367977	Present	Present	Present	Menke et al. (2009)
356	Urban	33.00470109	117.0437414	Present	Present	Present	Menke et al. (2009)
357	Urban	33.23094998	117.2272456	Present	Present	Present	Menke et al. (2009)
358	Urban	33.12025019	117.0682278	Present	Present	Present	Menke et al. (2009)
359	Urban	33.1052955	117.0711713	Present	Present	Present	Menke et al. (2009)
360	Urban	33.0319885	117.1084434	Present	Present	Present	Menke et al. (2009)
361	Urban	32.80273812	117.2508621	Present	Absent	Absent	Menke et al. (2009)
363	Urban	32.689444	− 117.191944	Present	Absent	Present	Menke et al. (2009)
364	Urban	32.77449418	117.0245181	Present	Present	Present	Menke et al. (2009)
366	Urban	32.83714182	117.2070247	Present	Present	Present	Menke et al. (2009)
367	Urban	33.29333	− 117.2078	Present	Present	Present	Menke et al. (2009)
368	Urban	32.68030089	117.0801106	Present	Present	Present	Menke et al. (2009)
369	Urban	32.96667	− 117.2311	Present	Present	Present	Menke et al. (2009)
370	Urban	32.73806	117.1471677	Present	Present	Present	Menke et al. (2009)
371	Urban	33.02056	− 116.9192	Present	Absent	Absent	Menke et al. (2009)
372	Urban	32.714167	− 116.877778	Present	Present	Present	Menke et al. (2009)
373	Urban	32.92208209	117.1482554	Present	Present	Present	Menke et al. (2009)

continued

Site no.	Environment	Latitude	Longitude	Original	2018 resurvey	2019 resurvey	Original study
374	Urban	32.84350512	117.0168972	Present	Present	Present	Menke et al. (2009)
375	Urban	32.90789693	117.0642621	Present	Present	Present	Menke et al. (2009)
376	Urban	32.58511647	117.0359302	Present	Present	Present	Menke et al. (2009)
377	Urban	32.67239671	117.0801714	Present	Present	Present	Menke et al. (2009)
38	Agriculture	32.9416842	116.8617957	Absent	Absent	–	Menke et al. (2009)
48	Agriculture	32.69802659	116.8637878	Absent	Absent	–	Menke et al. (2009)
84	Agriculture	33.26944	− 117.13	Absent	Absent	–	Menke et al. (2009)
101	Agriculture	33.22120263	116.9910299	Absent	Absent	–	Menke et al. (2009)
92	Agriculture	33.16348025	116.9745768	Absent	Present	–	Menke et al. (2009)
93	Agriculture	33.09083	− 117.0072	Absent	Present	–	Menke et al. (2009)
97	Agriculture	33.27139	− 117.0969	Absent	Present	–	Menke et al. (2009)
39	Agriculture	33.30842534	− 117.070988	Present	Present	–	Menke et al. (2009)
45	Agriculture	32.55809691	117.0903199	Present	Present	–	Menke et al. (2009)
58	Agriculture	32.949669	− 117.196505	Present	Present	–	Menke et al. (2009)
69	Agriculture	32.5477403	117.1000551	Present	Present	–	Menke et al. (2009)
73	Agriculture	33.03616318	117.2005621	Present	Present	–	Menke et al. (2009)
88	Agriculture	33.20513162	117.0873604	Present	Present	–	Menke et al. (2009)
98	Agriculture	33.22361	− 116.9986	Present	Present	–	Menke et al. (2009)
94	Agriculture	33.21059555	117.0349776	Present	Absent	–	Menke et al. (2009)
123	Agriculture	33.04857259	116.9699721	Present	Absent	–	Menke et al. (2009)
137	Natural	32.653889	− 117.149444	Absent	Absent		Menke et al. (2009)
203	Natural	33.42723625	117.2757346	Absent	Absent	–	Menke et al. (2009)
224	Natural	33.24619784	117.1011983	Absent	Absent	–	Menke et al. (2009)
184	Natural	33.26709068	116.9679717	Absent	Absent	–	Menke et al. (2009)
195	Natural	33.20733786	− 117.121293	Present	Present	–	Menke et al. (2009)
172	Natural	33.07778145	− 117.164595	Present	Present	–	Menke et al. (2009)
179	Natural	33.07143715	117.2761946	Present	Present	–	Menke et al. (2009)
229	Natural	33.17778	− 117.3419	Present	Present	–	Menke et al. (2009)
265	Natural	32.926389	117.2501587	Present	Present	–	Menke et al. (2009)
268	Natural	32.85176118	117.2294666	Present	Present	–	Menke et al. (2009)
270	Natural	33.07209375	117.2606577	Present	Present	–	Menke et al. (2009)
271	Natural	32.84151369	117.0366266	Present	Present	–	Menke et al. (2009)
129	Natural	32.978333	− 117.152222	Present	Present	–	Menke et al. (2009)
181	Natural	33.422792	117.2161843	Present	Absent	–	Menke et al. (2009)
1	Natural	33.35108	− 118.35285	Absent	Absent	–	Backlin et al. (2005)
2	Natural	33.35157	− 118.36586	Absent	Absent	–	Backlin et al. (2005)
6	Natural	33.35338	− 118.3966	Absent	Absent	–	Backlin et al. (2005)
7	Natural	33.38317	− 118.41092	Absent	Absent	–	Backlin et al. (2005)
8	Natural	33.37804	− 118.40788	Absent	Absent	–	Backlin et al. (2005)
9	Natural	33.41205	− 118.43466	Absent	Absent	–	Backlin et al. (2005)
10	Natural	33.42099	− 118.44016	Absent	Absent	–	Backlin et al. (2005)
12	Natural	33.40317	− 118.42457	Absent	Absent	–	Backlin et al. (2005)
13	Natural	33.40325	− 118.42501	Absent	Absent	–	Backlin et al. (2005)
3	Natural	33.34919	− 118.36586	Present	Absent	–	Backlin et al. (2005)
4	Natural	33.35709	− 118.36199	Present	Present	–	Backlin et al. (2005)

continued

Site no.	Environment	Latitude	Longitude	Original	2018 resurvey	2019 resurvey	Original study
5	Natural	33.36221	− 118.36256	Present	Present	–	Backlin et al. (2005)
11	Natural	33.40477	− 118.4119	Present	Present	–	Backlin et al. (2005)
14	Natural	33.39215	− 118.44243	Present	Present	–	Backlin et al. (2005)
15	Natural	33.3852	− 118.44581	Present	Present	–	Backlin et al. (2005)
16	Natural	33.37911	− 118.47865	Present	Present	–	Backlin et al. (2005)
17	Natural	33.3777	− 118.47877	Present	Present	–	Backlin et al. (2005)
18	Natural	33.41012	− 118.46689	Present	Absent	–	Backlin et al. (2005)
19	Natural	33.41806	− 118.4692	Present	Present	–	Backlin et al. (2005)
20	Natural	33.42712	− 118.47398	Present	Present	–	Backlin et al. (2005)

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