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RESEARCH ARTICLE



Invasion of the gall mite *Aceria genistae* (Acari: Eriophyidae), a natural enemy of the invasive weed *Cytisus scoparius*, into California, U.S.A. and predictions for climate suitability in other regions using ecological niche modelling

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ABSTRACT

Scotch broom (*Cytisus scoparius* (L.) Link) is a European shrub that has naturalised in several countries worldwide and is recognised as an invasive weed in much of western North America. The mite *Aceria genistae* (Nalepa) is a coevolved, gall-inducing herbivore associated with Scotch broom in its native range and has been intentionally introduced as a classical weed biological control agent of *C. scoparius* in Australia and New Zealand. An adventive, never intentionally introduced, population of *A. genistae* was discovered in Washington and Oregon, U.S.A. in 2005. Surveys for *A. genistae* in California resulted in the discovery of the gall mite in 11 counties, with a widely scattered distribution. Molecular and morphological assessments confirm the mites collected from galls in California are *A. genistae*. Whether natural or anthropogenic, the estimated rate of long range dispersal for *A. genistae* from Washington or Oregon to California ranges from 39 to 62 km/yr. Niche model predictions indicate that *A. genistae* will continue to expand its distribution throughout much of the Scotch broom-invaded lands of California but areas supporting the weed in the Eastern U.S.A. appear less suitable. Modelling evidence also indicates that portions of Chile and Argentina are suitable for colonisation by *A. genistae*, also suggesting that expansion of the mite is possible in areas of Tasmania, southeastern Australia, and New Zealand where the mite was released. The environmental safety of *A. genistae* in relation to non-target plants and the influence of herbivory on Scotch broom fitness are discussed.

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Scotch broom; biological control; spread; Maxent

Introduction

The shrub *Cytisus scoparius* (L.) Link, commonly known as Scotch broom, has a native range that extends from Great Britain across Europe to the Ural Mountains of Asia and

from Sweden south to the Mediterranean (Bossard & Rejmanek, 1994). The European native has been widely distributed globally, with exotic populations recorded in Australia, New Zealand, Canada, India, Iran, Japan, South Africa, Argentina, Chile and the United States (Hosking, Sheppard, & Sagliocco, 2012). The shrub was first introduced to the Pacific Northwest of the United States in the 1850s as an ornamental (Bossard & Rejmanek, 1994; Gilkey, 1957) but was also intentionally planted for erosion control (Gilkey, 1957; Schwendiman, 1977). Like other exotic broom species in the region, *C. scoparius* is a leguminous shrub that typically grows 1–3 m tall but can exceed 4 m (Coombs, Markin, & Forest, 2004). Naturalised populations of *C. scoparius* often form dense thickets and, as a result, the weed is regarded as a noxious pest in forests, rangelands and natural areas throughout the Pacific coastal region of North America from British Columbia through California.

Scotch broom invades undisturbed grass, shrub, and forested systems below 1300 m elevation in the Pacific coastal states but is also common in disturbed areas like river beds, road cuts, disturbed forests, and agricultural or pasture lands. Competitive superiority over most native flora is facilitated by high reproductive output and a long-lived seed bank. Moderately sized plants can produce thousands of seeds a year, which are self-dispersed through explosive dehiscence from the pea-shaped pods or moved by ants, rain or machinery (Bossard, 1991; Parker, 1997). Economic analyses indicate that Scotch broom invasions cost reforestation efforts an estimated \$47 million USD annually in Oregon (Coombs et al., 2004) and may cause up to \$142 million USD in lost revenue as well as 660 lost jobs in Washington per year (Cohen et al., 2017).

Classical weed biological control of *C. scoparius* in the United States was first implemented in the 1960s. Two specialist natural enemies, originating from the weed's native range, were released into the U.S.A.: the stem miner *Leucoptera spartifoliella* (Hubner) (Lepidoptera: Lyonetiidae) released in California in 1960 and the seed beetle *Exapion fusciostre* (Fabricius) (Coleoptera: Brentidae) released in California in 1964, in Oregon in 1983, and in Washington in 1989 (Coombs et al., 2004; Hosking et al., 2012). At least 10 other exotic herbivores also attack *C. scoparius* in the U.S.A. (enumerated in Coombs et al., 2004) but most notably *Bruchidius villosus* Fabricius (Coleoptera: Chrysomelidae), which was discovered in North Carolina but later intentionally released in Oregon and Washington. This suite of natural enemies, while limiting the annual seed crop, do not collectively provide sufficient population regulation to alter the prevalence or invasion trajectory of *C. scoparius* in western North America (Coombs et al., 2004; Parker, 2000).

A research programme targeting *C. scoparius* conducted by New Zealand and Australian scientists included the investigation of the European broom gall mite *Aceria genistae* (Nalepa) (Acari: Eriophyidae) as a candidate biological control agent of the invasive plant. Following nearly a decade of improving rearing methodologies, host range testing, removing secondary contaminants, and clarifying taxonomic uncertainty (Sagliocco et al., 2011; Xue, Han, & Zhang, 2015), *A. genistae* was deemed sufficiently host specific for introduction and was released in New Zealand in 2007 and Australia in 2008–2010 (Hosking et al., 2012; Paynter, Gourlay, Rolando, & Watt, 2012). The mite established in both countries, with 100s of individual galls developing on attacked plants in some areas and early evidence of stem dieback on plants with high gall densities (Sagliocco et al., 2011).

Surprisingly, an adventive population of *A. genistae* was discovered in 2005 near both the cities of Tacoma, in western Washington, and Portland, Oregon, U.S.A. (Andreas et al., 2013; Smith, de Lillo, & Amrine, 2010). This extension of the herbivore's geographic range to North America inspired surveys for the mite in *C. scoparius*-infested areas of British Columbia, Canada, and the states of Washington, Oregon, and California. The objectives of this research were to: (1) document the invasion of *A. genistae* into California, (2) confirm the identification of gall mites on *C. scoparius* in California, (3) quantify dispersal patterns, and (4) predict the potential geographic distribution of *A. genistae* using niche modelling. This paper is one in a series of articles that document the invasion and impact of *A. genistae* on *C. scoparius* along the Pacific coastal region of North America.

Materials and methods

Identifications

Eriophyid mites were extracted from galled *C. scoparius* plant material originating from California, Australia, and New Zealand for taxonomic comparison with Washington and Oregon specimens identified previously (Andreas et al., 2017). Specimens were slide-mounted in polyvinyl alcohol on microscope slides, examined with a Leica DM5500B phase contrast microscope, and photos were taken with a Leica DFC420 camera attached to a trifocal lens. Morphological measurements were taken via Leica Application Suite software 4.2, and specimens were identified to species by comparison with the taxonomic literature (Baker, Kono, Amrine, Delfinado-Baker, & Stasny, 1996; Xue et al., 2015). Voucher specimens are deposited as slide-mounted specimens in the Systematic Entomology Laboratory Collection, Beltsville MD, U.S.A., and the Canadian National Collection of Insects, Arachnids and Nematodes, Ottawa, Canada.

Mites within galls were studied with Low Temperature Scanning Electron Microscopy (LT-SEM) at the United States Department of Agriculture (USDA), Agricultural Research Service (ARS) Bioproducts Research Unit, Characterization Facility (Albany, CA, U.S.A.) following Ochoa, Beard, Bauchan, Kane, and Dowling (2011) with the following exceptions: observations were performed using an S-4700 field emission SEM (Hitachi High Technologies America, Inc., Japan) equipped with a Alto 2500 (Gatan, Inc., Pleasanton, CA) cryotransfer system. Each gall was dissected to expose mites and the dissected gall was placed directly onto a cryotransfer holder consisting of 16 × 30 mm copper plate that contained a layer of Tissue-Tek OCT Compound (Sakura Finetek USA Inc., Torrance, Cal., USA), which acted as a cryo-adhesive upon freezing. The samples were frozen in liquid nitrogen in the slush chamber of the Alto 2500 system. After 20–30 sec, the holders containing the frozen samples were transferred under vacuum directly to the preparation chamber of the Alto 2500 system. Removal of any surface contamination (condensed water vapour) took place in the preparation chamber by sublimation of surface water from the frozen specimens for 10–15 min by raising the temperature of the preparation chamber stage to –90°C. Following sublimation, the temperature was lowered to less than –135°C and was sputter-coated with gold-palladium in the preparation chamber. The specimens were transferred to the cryo-stage inside the SEM chamber via the Alto 2500 interlock system for observation and photography. The cryo-stage was maintained below –135°C to avoid further sublimation of surface water. An accelerating

voltage of 2 kV was used to view and photograph the specimens. Images were captured at 2560×1920 dpi using a Quartz imaging system (Vancouver, B.C., Canada). The LT-SEM images were helpful with reinforcing some of the morphological observations made under light microscopy.

Genomic DNA was extracted from whole specimens (10 mites per extraction) for 24 h using a DNeasy Tissue kit (Qiagen, Inc., Santa Clara, California, USA). Following extraction, genomic DNA was purified following the DNeasy Tissue kit protocol. PCR amplifications were performed using the protocol described in Knee (2017) and primer pairs LCO1490 + HCO2198 (Folmer, Black, Hoeh, Lutz, & Vrijenhoek, 1994). Amplified products and negative controls were visualised on 1% agarose electrophoresis gels and purified using pre-cast E-Gel CloneWell 0.8% SYBR Safe agarose gels (Invitrogen, Carlsbad, California, USA). Sequencing reactions followed the protocol of Knee, Beaulieu, Skevington, Kelso, and Forbes (2012) and sequencing was performed at the Agriculture and Agri-Food Canada, Eastern Cereal and Oilseed Research Centre Core Sequencing Facility (Ottawa, Ontario, Canada). Sequence chromatograms were edited and contiguous sequences were assembled using Sequencher v5.3 (Gene Codes Corp., Ann Arbor, Michigan, USA). COI sequences were aligned manually in Mesquite v3.10 (Maddison & Maddison, 2016) according to the translated amino acid sequence. Sequences generated during this study have been submitted to GenBank (MH885462–MH885468).

Survey methods and quantifying dispersal

Surveys for *A. genistae* were conducted from 2010 through 2017 and ranged from the California-Oregon border to Los Angeles County in southern California (Figure 1). Feeding by the mite transforms meristematic buds into diagnostic galls that disclose the presence of the otherwise cryptic colonies, even at very low population densities. Galls are characterised as deformed foliar tissue that collectively forms a round, pubescent mass arising from a foliar bud (Sagliocco et al., 2011; Figure 2). Therefore, surveys for *A. genistae* focused on searching for these diagnostic galls on plants within *C. scoparius* stands. Surveys were conducted haphazardly and with differing levels of effort, starting in 2010 when multiple *C. scoparius* patches in El Dorado County, California, were opportunistically surveyed in conjunction with other research activities. The same patches in El Dorado County, in addition to several stands of *C. scoparius* in Siskiyou County, were surveyed in 2014. During the subsequent three years (2015–17), however, annual systematic surveys were made in 14 counties where *C. scoparius* invasion is most problematic (Figure 1). General survey protocols included using herbarium records or expert knowledge to locate *C. scoparius* infestations, examining vegetation for mite galls for ca. 30 min per observer, scoring the site based on the presence or absence of galls, and recording the coordinates of the location with a global positioning system (GPS) device. The search area was generally limited to a 50 m radius within the starting point. Once discovered, the leading edge of the population was quantified along transects radiating either North–South or East–West based on accessibility. Surveys for galls were extended until the absence of *A. genistae* (inferred from the absence of its galls) was consistently observed (Paynter et al., 2012; Pratt, Slone, Rayamajhi, Van, & Center, 2003).

In addition to these formal survey methods, a community-based online reporting effort was also implemented. This effort involved training citizen-scientists familiar with

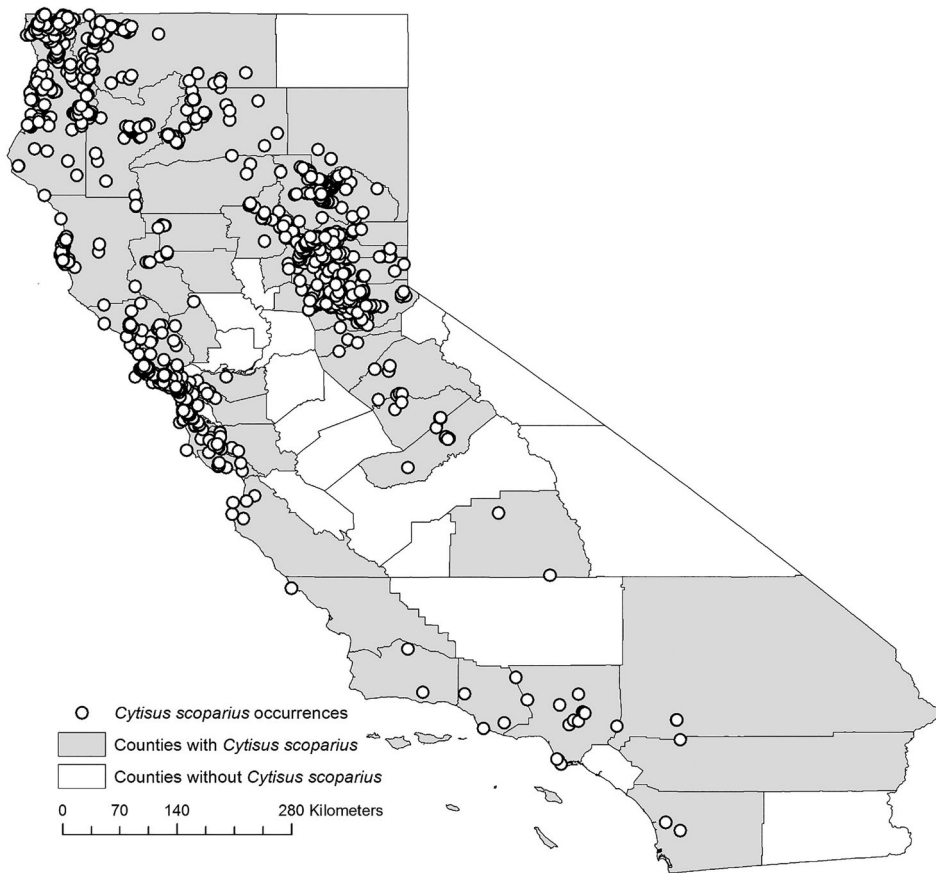


Figure 1. Geographic distribution of Scotch broom, *C. scoparius*, in California based on herbarium records.

C. scoparius to identify *A. genistae* galls and report occurrences with corresponding GPS information through a web-based interface. Trained observers confirmed online reports that represented new foci. In this manner, a growing database of *A. genistae* occurrence across the landscape was created through systematic surveys and online reporting from land managers (user input: <http://ucanr.edu/survey/survey.cfm?surveynumber=13262> and the resulting database: <https://tinyurl.com/zwm5ykd>). Rates of spread were calculated based on the earliest detection of *A. genistae* in Washington and Oregon. It is assumed that the first reports *A. genistae* in North America represent the initial colonisation sites but it remains unknown if there are other, earlier colonisation events that went unrecognised and, therefore, caution should be used when interpreting these long distance rates of spread.

A separate survey was designed to examine if gall size and density per plant occurring near the centre of geographically large, contiguously galled areas (hereafter referred to as central) differs from those along a population's leading edge or at a new satellite area where new founding populations are first detected (hereafter referred to as edge). Assessments were done during 2017 at six central locations, at the north and south leading edges

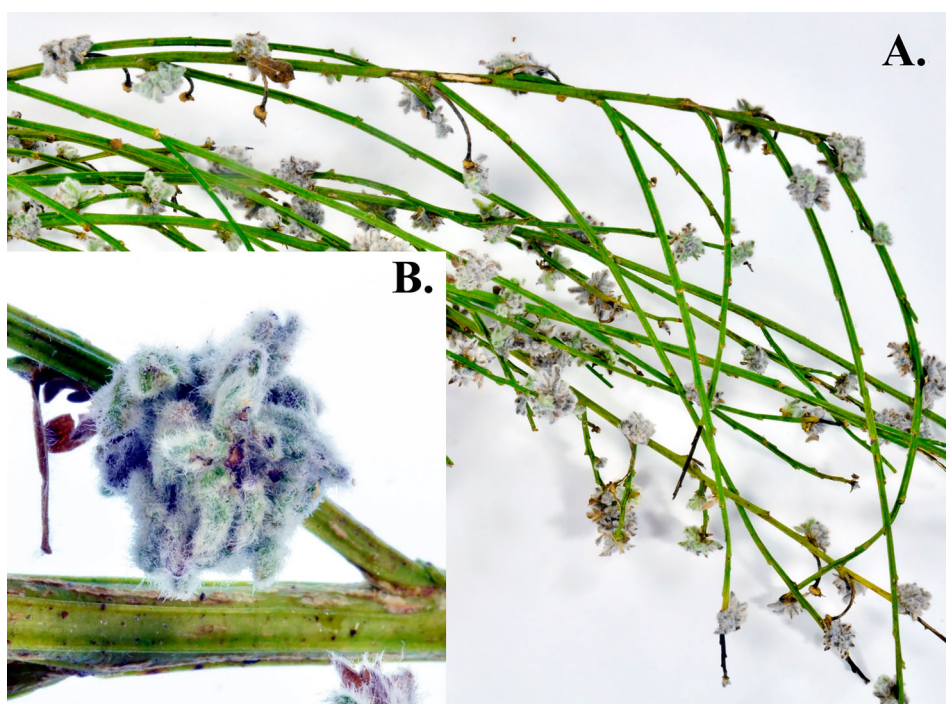


Figure 2. *Aceria genistae* galls on *C. scoparius*. A. Light coloured galls produced at foliar axils along branches. B. Close up of gall.

of a large coalesced population, and at four founding *A. genistae* populations that were geographically small (=edge) as well as distant from neighbouring foci. Assessments included randomly selecting 10 individual plants at each sampled site (10 plants * 12 sites = 120 plants), categorising selected plants based on visually estimated gall number, and measuring the diameter of only the largest gall observed on each plant. Gall density categories included: 0 = no galls, 1 = ≤ 10 , 2 = 11–50, 3 = 51–100, 4 > 100 galls per plant. Gall diameters were measured in two opposite directions, the average radius was determined, and the volume of the gall was calculated as a sphere $V = 4/3\pi r^3$. Gall data from central and edge populations were compared with ANOVA followed by Tukey HSD post hoc analyses (Littell, Stroup, & Freund, 2002). All data are presented as means \pm standard error (S.E.).

Niche modelling and predicted range

The potential distributions of *A. genistae*, *C. scoparius* and the resulting overlap of the two species were modelled based on climate suitability with the software package Maxent, version 3.3.3k (Phillips, Anderson, & Schapire, 2006). Presence data (GPS coordinates) for *A. genistae* were collected both from field surveys in the U.S.A. (California, Oregon, and Washington) and New Zealand as well as published presence data from Australia, New Zealand, France, Italy, Germany, the United Kingdom, and Spain, totalling 135 unique data points (GBIF, 2016; Xue et al., 2015). Occurrence data for *C. scoparius* was

acquired from the Global Biodiversity Information Facility's website and accounted for 22,575 unique GPS points. These occurrences spanned Europe (Andorra, Austria, Belgium, the Czech Republic, Denmark, Estonia, Finland, France, Germany, Ireland, Italy, Luxembourg, the Netherlands, Norway, Poland, Portugal, Slovenia, Slovakia, Switzerland, Spain, Sweden, the UK), North America (the United States, Canada), Central and South America (Argentina, Bolivia, Brazil, Chile, Ecuador, Peru), Africa (Morocco, Madagascar, South Africa), Oceania (Australia, New Zealand), and Japan. Additional data covering California were obtained from the Consortium of California Herbaria (2017).

Altitude and 19 bioclimatic variables were downloaded in 2.5 arc-minute resolution raster format from WorldClim's online database (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005; accessible at <http://www.worldclim.org>). These data were interpolated from weather station data and are derivations of temperature and precipitation variables that often serve as critical factors determining, in part, a species geographic range (Hijmans et al., 2005). Akaike information criteria (AIC) and sample size corrected Akaike information criteria (AIC_c) analysis were run using ENMTools to find the variable combination that best fit the given data (Akaike, 1973; Hurvich & Tsai, 1989; Warren & Seifert, 2011; Warren, Glor, & Turelli, 2010). For both species, models using all 20 of WorldClim's variables (altitude and the 19 bioclimatic variables) were markedly more accurate by both AIC_c and AIC analysis, relative to models with fewer variables.

For the most part, default Maxent settings were used (Mukherjee, Diaz, Thom, Overholt, & Cuda, 2012; Peterson, Papes, & Eaton, 2007; Rinnhofer et al., 2012). The full globe was set as the model background and 10,000 pseudo-absence points were randomly selected. For statistical testing purposes, the models were run 10 times with random seeded subsampling: 70% of the dataset randomly selected for training to build the models and the remaining 30% selected for testing (Mukherjee, Christman, Overholt, & Cuda, 2011). For the final visualisation of distribution overlap, one model for each species was created with the full dataset partitioned towards training, in order to achieve the highest degree of accuracy possible given the available data (Mukherjee et al., 2011). To simplify comparison of the two species' ranges, the continuous climate suitability values of the outputs were converted to binary values differentiating suitable/unsuitable regions. This conversion required the use of a threshold; maximum sum of sensitivity and specificity (max SSS) was selected as recommended by Liu, White, and Newell (2013). The max SSS of training data (as opposed to max SSS of test data) was used due to more data being partitioned for training versus test purposes. ArcMap's Raster Calculator tool was used to calculate the potentially suitable areas, which were defined as the range overlap of the two binary suitability outputs (ESRI, 2014).

The resulting models were tested using 1-tailed binomial p-tests to determine whether predictions were significantly better than a random prediction with the same fractional predicted area. The models' omission rates were also tested. Threshold-independent receiver operating characteristic (ROC) testing, or area under curve (AUC), a commonly reported metric of model accuracy in SDMs (Pearson et al., 2006; but see Lobo, Jiménez-Valverde, & Real, 2008) was done within Maxent.

Results

Taxonomic determination

Both molecular and morphological assessments indicate that the mites collected from galls in California are *A. genistae* (Figure 3). Mite populations from *C. scoparius* galls collected from California (2016), Tasmania (2016) and New Zealand (2016) are morphologically essentially identical to each other, and are compatible with the descriptions of *A. genistae* in Xue et al. (2015) and Han, Hong, and Zhang (2016). A 681 bp fragment of COI was

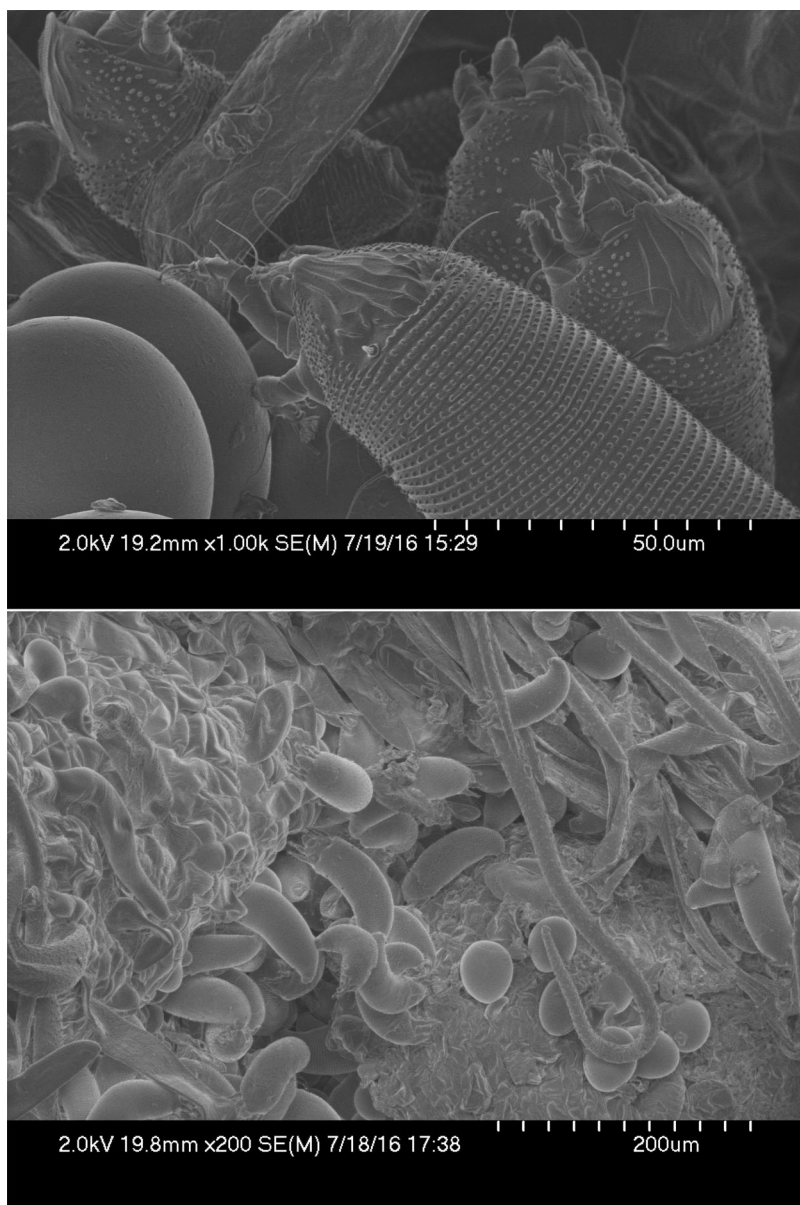


Figure 3. Low temperature scanning electron microscopy of *A. genistae*.

amplified from seven *A. genistae* samples extracted from *C. scoparius* galls from California (2016), Tasmania (2016) and New Zealand (2016). Intraspecific divergence amongst the seven samples was 0–2.2%, with mites from the New Zealand and California samples more closely related to each other (0% divergence) than to those from the Tasmania sample (2.2% between Tasmania and the two other samples).

Surveys and dispersal

No *A. genistae* galls were discovered through intermittent monitoring of *C. scoparius* stands in El Dorado County from 2010 and 2014. A population of *A. genistae*, however, was discovered nearly 300 km south of the Oregon border in April 2014 when a land manager observed abnormal growth on *C. scoparius* plants near Georgetown, El Dorado County, California, and contacted the regional United States Forest Service office and University of California Cooperative Extension service for diagnosis. A site visit revealed galls visually similar to those produced by *A. genistae* as reported in the literature (Hosking et al., 2012; Paynter et al., 2012). The citizen-scientist reporting system resulted in the collection of 39 unique GPS data points for the occurrence of *A. genistae*. These reports focused primarily on Nevada, Placer, and El Dorado counties due to focused outreach to land managers in that region. Surveys conducted in 2015–17, augmented by these online reports, revealed a distribution of *A. genistae* across seven counties (Plumas, Yuba, Butte, Sierra, Nevada, Placer, El Dorado, and Amador) along the western foothills of the Sierra-Nevada Mountains (Figure 4).

Galls in more northerly regions of the state among the Klamath and Cascade Mountains were first observed in June 2014, with discoveries near the towns of Mount Shasta, French Gulch (Shasta County), and Happy Camp (Siskiyou County; Figure 4). Additional galls were observed just south of the Oregon state border, in California's most northwesterly county of Del Norte in August 2017. A third area of *A. genistae* invasion was discovered in August 2015 near Mendocino (Mendocino County) within the California Coastal Range, approximately 178 km from the more northerly Shasta population and 215 km from the eastern populations (Figure 4). No *A. genistae* galls were discovered in other *C. scoparius* infested counties during the 2015–17 surveys.

Cytisus scoparius plants varied widely both in their level of attack and the size of galls within their canopies between sample sites in California. However, for geographically large populations, galls are larger and more numerous (density per plants) in the centre of these populations than on their edge. The mean gall density category for plants in the centre of geographically large populations was 2.0 (± 0.18), which corresponds to 11–50 galls per plant. In contrast, the mean gall density was lower for plants at the geographical edge, with a gall density category of 1.2 (± 0.16) that corresponds with ≤ 10 galls per plant ($F_{1, 118} = 11.58$; $P = 0.0009$). Similarly, the volume of the largest galls observed within a plant's canopy was more than five-fold greater for centrally located ($1677.7 (\pm 706.7) \text{ mm}^3$) versus edge colonies ($327.7 (\pm 87.7) \text{ mm}^3$; $F_{1, 118} = 8.85$; $P = 0.0036$).

Assuming California populations of *A. genistae* are derived from dispersing individuals that spread south from Washington and Oregon, the gall mite has moved ca. 587 km over 15 years or 39 km/yr when measuring spread from Tacoma, WA to the

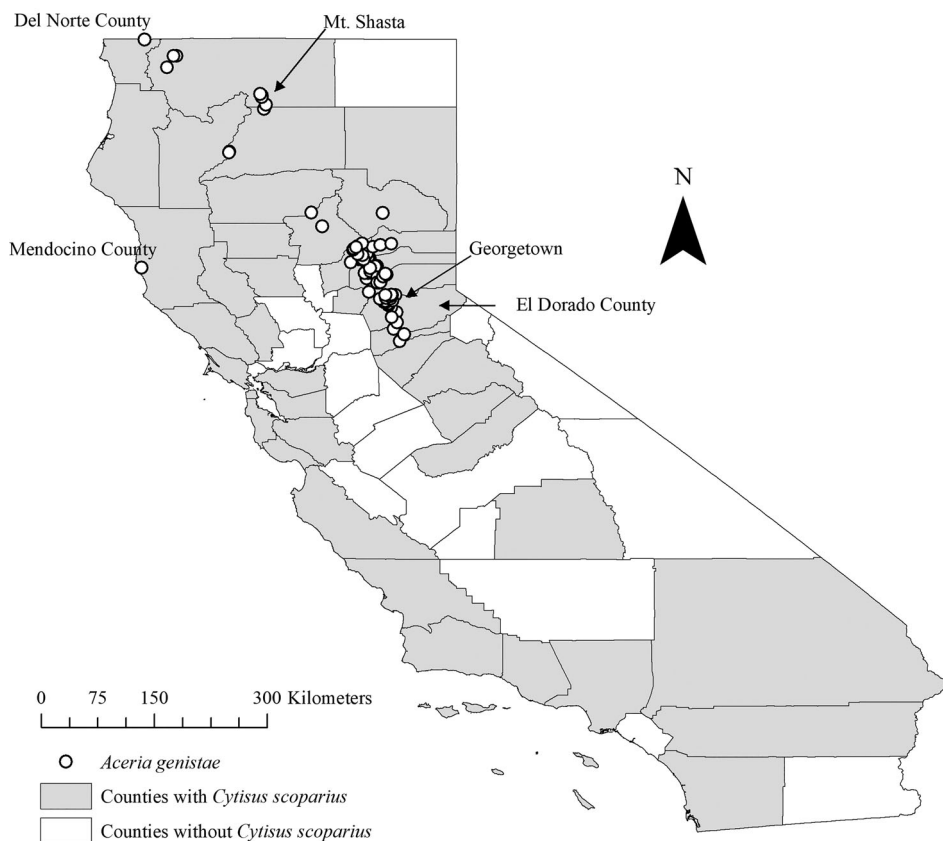


Figure 4. Geographic distribution of the adventive European gall mite *A. genistae* in relation to its host Scotch broom in California.

most northern observed populations of the mite in northern California. An alternative scenario, which may be supported by differences in gall size and density, is that one of the earliest arrivals of *A. genistae* in California occurred in El Dorado County, centred on Georgetown, resulting in a dispersal distance of 936 km. Based on the assumption that Georgetown is an early invasion point, dispersal from Washington to California is ca. 62 km/yr. No appreciable annual spread was observed locally when measuring short-range dispersal along *A. genistae* invasion fronts, except in the southern direction from the Mount Shasta area where new galls were observed 21 km south of the previous year's census.

Niche modelling and predicted range

All replicated binary maximum entropy models for *A. genistae* and *C. scoparius* were significantly better than random ($P < 0.001$). Test omission values for *A. genistae* averaged 0.027 (range 0–0.081) and 0.013 (range 0.009–0.018) for *C. scoparius*. Mean test AUC values for *A. genistae* models were 0.993 (range 0.988–0.995) but markedly lower for *C. scoparius* (0.69, range 0.689–0.701), indicating the model is less predictive of the plant's

distribution. These models suggest that much of the *C. scoparius* invaded areas in northern California are suitable for colonisation by *A. genistae*, a region with strong validation data as reported herein (Figure 5). Areas of central and southern California appear less suitable for *A. genistae*, particularly along the coast and the southern extent of the Sierra Nevada mountain range (Figure 5) where the host occurs but the mite may be poorly adapted to colonise. Suitable areas for both species increase north of California, with much of the *C. scoparius* habitat predicted to be suitable for the gall mite colonisation (Figure 5). However, portions of the eastern Cascade Mountain Range appear less suitable for the mite as well as nearly all the coastline and portions of Vancouver Island in British Columbia (Figure 5). Although not represented graphically, projections were developed for the

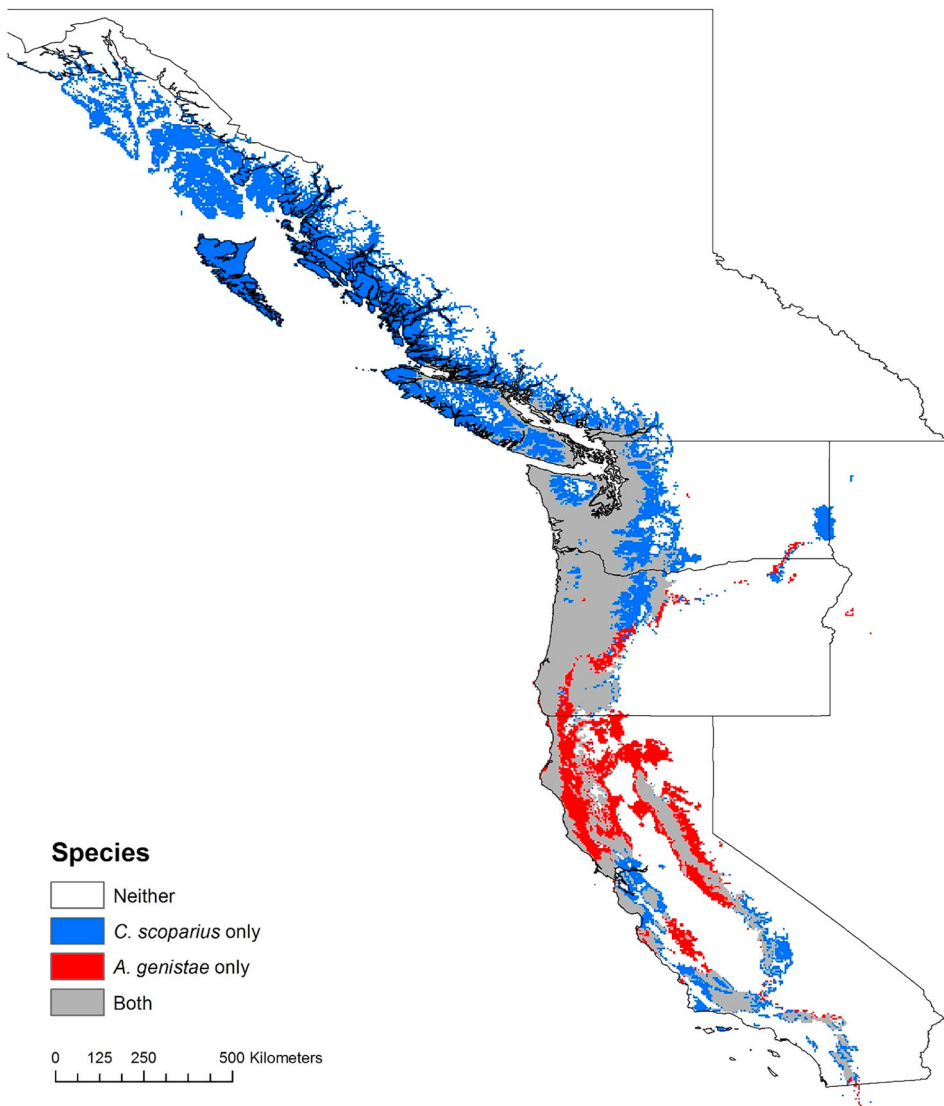


Figure 5. Potential geographic range and overlap of *A. genistae* and *C. scoparius* in Western North America as predicted from maximum entropy modelling.

Eastern U.S. (Virginia, North Carolina, South Carolina, and Georgia) where *C. scoparius* is established, but none of the replicated models indicated these areas as suitable for *A. genistae* ($P > 0.159$).

Maximum entropy models also predict that areas of Chile and Argentina in South America that could be potentially colonised by *C. scoparius* are also climatically suitable for colonisation by *A. genistae*, including coastal regions of central Chile from Santiago

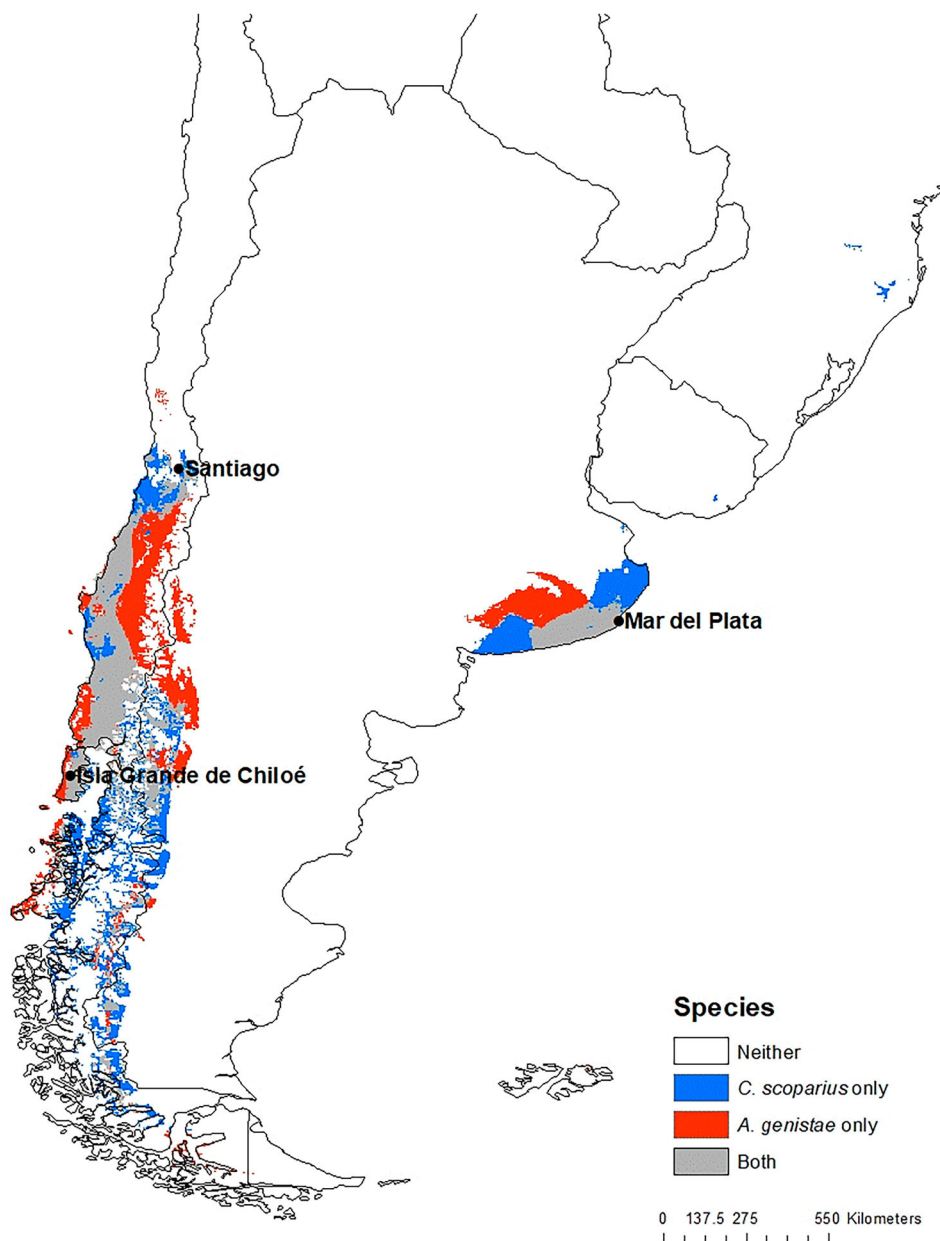


Figure 6. Predicted range and overlap of *A. genistae* and *C. scoparius* in South America as predicted from maximum entropy modelling.

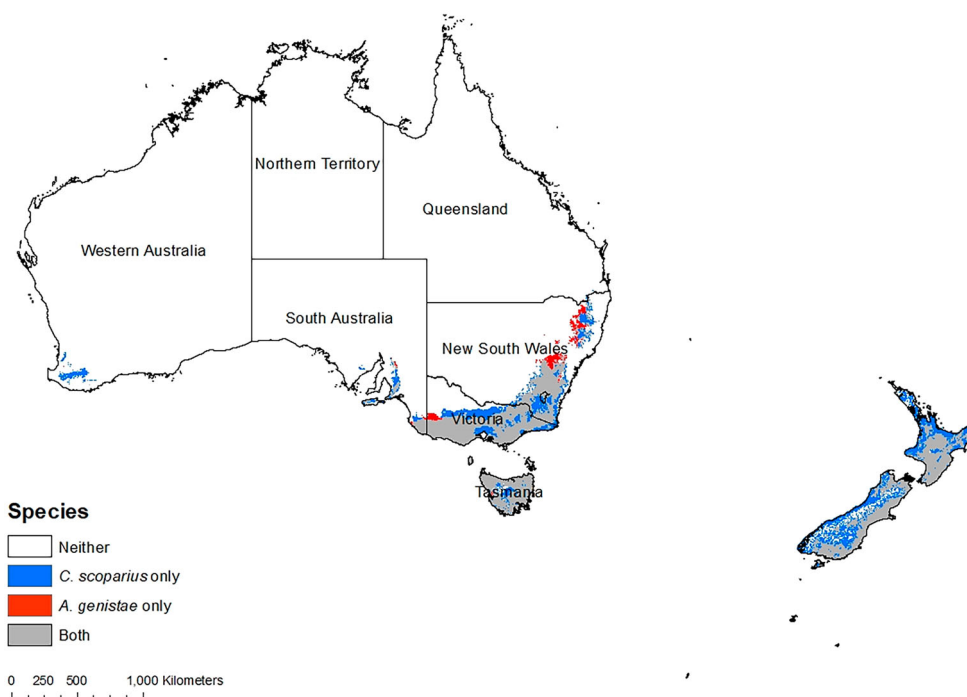


Figure 7. Potential geographic range and overlap of *A. genistae* and *C. scoparius* in Australia and New Zealand as predicted from maximum entropy modelling.

south to the Isla Grande de Chiloé as well as small patches in the southern Andes Mountains (Figure 6). Climate suitability is also favourable for *A. genistae* along a small portion of Argentina's eastern coastal region near the town of Mar de Plata and extending inland (Figure 6). Similar results were observed when models were projected for Australia and New Zealand (Figure 7). Consistent with the realised range of the gall mite, models predict much of Tasmania as suitable for *A. genistae* as well as much of the southern coastal areas of Victoria and New South Wales of Australia's mainland (Figure 7). The eastern coast of New Zealand and much of the North Island also appear suitable for colonisation by *A. genistae* (Figure 7).

Discussion

This is the first report in the scientific literature that documents the arrival of *A. genistae* in California, where the gall-inducing mite is currently limited to 11 counties (Figure 4). The highest concentration of colonised *C. scoparius* stands occur in a five-county area in the western foothills of the Sierra Nevada Mountains, which encompasses the first discovery of galled plants near the town of Georgetown (Figure 4). Smaller patches of galled plants are present near Mount Shasta, across the northern state boundary, and a small patch discovered on the northern coastal area near the town of Mendocino (Figure 4). This disjunct distribution of the mite in California is curious and raises several questions regarding dispersal pathways.

Ambulatory dispersal of eriophyid mites provides limited means of relocating to new host plants or host patches as local resources decline (Melo et al., 2014b). It is generally agreed, therefore, that eriophyid mites use primarily air currents for both short and long-distance dispersal, although phoresy, at least accidental, might occasionally favour long distance dispersal (Melo, Lima, Sabelis, Pallini, & Gondim, 2014a; Michalska, Skoracka, Navia, & Amrine, 2010). Aerial dispersal may be facilitated by behaviours that increase the probability of being carried aloft into the air currents (Melo et al., 2014a). The resulting diffusion of mites across the landscape is, therefore, largely influenced by wind, meteorological factors, and geomorphology of the surrounding landscape. Although unlikely, the invasion of *A. genistae* to the western U.S.A. may be the result of multiple long-range aerial dispersal events originating from the mite's European native range, and because of that, *A. genistae* colonies in California may share no lineage with those of Washington or Oregon. An alternative explanation for the mite's arrival in California includes *A. genistae* colonising *C. scoparius* plants in Washington and Oregon from an unknown source but passively dispersing on wind currents south to California's most northerly counties prior to colonising the more southerly Sierra Nevada foothills. We hypothesise that gall densities and gall size provide insights to colonisation chronology based on the assumption that these parameters correlate with time of arrival. Whole plant estimates indicate that plants in central areas of large patches have higher densities of galls than plants along the spreading front or small colonies. Additionally, the largest galls observed on plants had markedly greater volume in central versus edge populations. These data provide limited evidence that the Sierra Nevada foothills were colonised by *A. genistae* prior to areas along the state's northern border or coast (Figure 4). The distribution of galled *C. scoparius* plants across this seven-county area in the Sierra Nevada region occurs at a higher gall density per plant, with populations largely coalesced and clear invasion fronts were observed at the northern and southern extremes of the mite's distribution in this area (Figure 4). Therefore, an alternative explanation for the mite's distribution in California may be human-facilitated movement from areas of galled *C. scoparius* lands in Oregon or Washington into the Sierra Nevada area. El Dorado County, along with other neighbouring counties, includes actively forested lands and the movement of timber equipment between Oregon or Washington and California is not an uncommon occurrence. Galls or mites may have been transported inadvertently to *C. scoparius* infested lands in the Sierra Nevada foothills, resulting in the observed scattered distribution, with the largest galls ca. 200 km south and east of the much smaller satellite foci (Figure 4).

Regardless of dispersal pathway, these data underscore the long-range dispersal abilities of *A. genistae* and the permeability of spatial and geographical constraints (Pratt & Center, 2012). Emigration of *A. genistae*, through inherent or anthropogenic means, was not restricted by mountain ranges or extended expanses of host-free lands. *Aceria genistae* has spread from the Canadian province of British Columbia to northern California following its discovery in 2005, a distance of approximately 1500 km. The mite has established colonies across a wide range of climatic conditions in California, from 18 to 1160 m above sea level, including coastal populations <3 km from the Pacific Ocean, in the moist Klamath National Forest, and the drier Sierra Nevada foothills (Figure 4).

The rate of dispersal for *A. genistae* remains difficult to quantify. Based on the data reported herein, local dispersal by *A. genistae* in California is generally limited. The

moving front of galled plants at monitored sites did not expand appreciably during the 2015–17 period. This slow dispersal rate is consistent with reports from New Zealand, where mites moved 33.4 (± 15.2) m/yr from 2008 to 2012 (Paynter et al., 2012). One notable long-range dispersal event was observed near the town of Dunsmuir, however, and this jump distance was 21 km. Long-range dispersal of *A. genistae* from Washington or Oregon to California, whether natural or anthropogenic, ranged from 39 to 62 km/yr and it may be hypothesised that the mite will disperse at a similar rate as it continues to move south in California (Figure 5). It appears likely that environmental conditions, including high levels of humidity, are critically influential to successful colonisation during dispersal events and may explain in part the variability in dispersal events observed herein (Paynter & Shaw, 1997).

The predicted geographic extents of *C. scoparius* and *A. genistae* are influenced by the accuracy of maximum entropy modelling. For instance, the AUC scores for *C. scoparius* models are lower than desired but also not surprising: AUC values are affected by the model's selected geographic range, particularly when the range includes areas well beyond the species' known distribution (Termansen, McClean, & Preston, 2006). For this reason, AUC values for species with widespread geographic distributions, such as *C. scoparius*, are often low (Lobo et al., 2008). Although the range of *C. scoparius* may continue to expand, its exotic ranges have been well established for over a century (Peterson & Prasad, 1998; Potter, Kriticos, Watt, & Leriche, 2009). These models have relevance to the potential expansion of the exotic weed in the regions of interest and support other models that predict greater potential ranges than are currently recorded (Potter et al., 2009). Much of the area predicted to be suitable for *A. genistae* falls within the predicted *C. scoparius* geographic range, but should not be interpreted as though the mite and host plant have symmetrical ranges. *Aceria genistae* appears to have a smaller potential range than *C. scoparius* overall, particularly in northern latitudes where only rare occurrences were predicted above 52 degrees north latitude in North America and 58 degrees north latitude in Europe (with the exception of Great Britain). Despite this, models predict that suitable environments for *A. genistae* include some of the most heavily *C. scoparius*-infested regions of the Pacific coast in North America, Chile, southern Australia, and New Zealand (Figures 5–7). Caution should be used when drawing inferences from these data, however, as models predict larger distributions for *C. scoparius* than currently exist, possibly resulting in an overestimation of suitable habitat if the exotic host plant does not continue to expand its geographic range (Figure 7).

Model predictions indicate that *A. genistae* will continue to expand its distribution throughout much of the *C. scoparius* stands in California as areas suitable for colonisation are common (Figure 5). The majority of *C. scoparius*-invaded region appears suitable for colonisation by *A. genistae* in Washington and Oregon except areas of lower elevations along the eastern side of the Cascade Mountains as well as much of British Columbia. The accuracy of the model to predict the mite's full geographic range remains unclear. There is no model-based evidence that *A. genistae* will colonise *C. scoparius* plants in the southeastern U.S.A., including the states of Virginia, North Carolina, South Carolina, and Georgia. This finding is surprising considering that other natural enemies, first released or discovered in the western states, have colonised the eastern populations of the exotic weed (Wheeler, 2017). The specialist psyllids *Arytainilla spartiophila* (Foerster) and *Arytaina genistae* (Latreille) are adventive to North America, the beetle *B. villosus* was

released as a biological control agents of *C. scoparius* in the Pacific Northwest in 1998. All three species have expanded their geographic distribution to include the eastern U.S.A. (Pfeiffer, 1986; Redmond, Forrest, & Markin, 2000; Wheeler, 2017; Wheeler & Hoebeke, 2004).

Model predictions also indicate that *C. scoparius*-invaded areas beyond North America may also be suitable for colonisation by *A. genistae* (Figures 6–7). Scotch broom is an invasive plant in South America, particularly in Chile and to a lesser degree in eastern Argentina (Peterson & Prasad, 1998; Potter et al., 2009). Modelling evidence indicates that portions of these invaded ranges are suitable for colonisation by *A. genistae* (Figure 6). The model identified Tasmania, southeastern Australia, and much of New Zealand as suitable for colonisation by *A. genistae*. However, these predicted distributions overestimate the known distribution of *A. genistae* following its release in 2008 (Paynter et al., 2012; Sagliocco et al., 2011). As before, it remains unclear if this overestimation is related to continued expansion of the mite over time or inaccuracies in the model.

The presence of *A. genistae* in California also raises concerns for host specificity of the adventive mite and risks it may pose to native flora. Unlike most adventive herbivores, the physiological host range of *A. genistae* is well understood as it was investigated prior to its intentional releases in New Zealand and Australia (Paynter & Shaw, 1997; Sagliocco et al., 2011). Eriophyoid mites are often host-specific herbivores, with 95% of mite species known from a single plant genus (Rector, Ashley, Gaskin, & Longland, 2013; Rosenthal, 1996; Skoracka, Smith, Oldfield, Cristofaro, & Amrine, 2010; Smith et al., 2010; Xue et al., 2015). Consistent with this trend, *A. genistae* was presented with 43 potential hosts that ranged in phylogenetic relatedness to *C. scoparius* but mites failed to persist on any plant tested except the target weed, providing strong evidence that the California native *Lupinus polyphyllus* Lindl and other close relatives do not fall within the physiological host range of the mite (Paynter & Shaw, 1997; Sagliocco et al., 2011). It should be noted that minor abnormalities in bud development were observed on the ornamental variety *Cytisus* ‘Crimson King’ and *Chamaecytisus palmensis* (Christ) F.A. Bisby & K.W. Nicholls as well as the closely related *Spartium junceum* L., but *A. genistae* failed to persist on these plants. These data clearly indicate that *A. genistae* has a narrow host range but additional data documenting host fidelities of the mite in relation to other California natives are needed, particularly in light of the recent recovery of *A. genistae* from experimental inoculations on *Cytisus striatus* (Hill) Rothm. and *Lupinus albicaulis* Douglas under field conditions and *Lupinus densiflorus* Benth from a greenhouse study in Washington (Andreas, 2010; Han et al., 2016). Haphazard assessments of the other exotic broom species established in California and Washington, including Portuguese broom (*C. striatus* Rothm.), French broom (*Genista monspessulana* (L.) L. Johnson), and Spanish broom (*S. junceum* L.) growing near galled *C. scoparius* plants, resulted in no observations of galls or gall-like structures on these sympatric weeds. A formal host range test, including no-choice evaluations of herbivore feeding and galling, will be conducted in future studies designed to quantify the safety of the mite in regard to flora in the Pacific coastal states of the U.S.A.

While these data provide insights to the establishment and distribution of *A. genistae* in California, little is known concerning the cost of gall formation and herbivory on the fitness of *C. scoparius*. Clearly some galling organisms can directly affect plant fitness through attack of flowers, fruits and seed (Stone & Schönrogge, 2003). A growing body

of literature also indicates that galls can indirectly influence plant performance by redirecting photosynthetic resources away from plant reproduction, growth, and storage and into gall tissue to support large populations of herbivores (Stone & Schönrogge, 2003). For instance, galls induced by the mite *Aceria malherbae* Nuzzaci on newly developing leaves and stems of *Convolvulus arvensis* L., can result in a $\geq 90\%$ biomass reduction of the exotic weed in Texas and Oregon (Smith et al., 2010). Limited studies indicate that leaf gas exchange and photosynthesis are significantly affected by eriophyoids, including gall-inducing species (Larson, 1998; Patankar, Quinton, & Baltzer, 2013). Future research will investigate the influence of herbivory and gall formation by *A. genistae* on growth and reproduction of *C. scoparius*.

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