Local grassland restoration affects insect communities

JUSTIN C. LUONG,[1,2] PATRICK L. TURNER,[1] CELINA N. PHILLIPSON[3] and KATJA C. SELTMANN[2] [1]Environmental Studies Department, University of California, Santa Cruz, California, U.S.A., [2]Cheadle Center for Biodiversity and Ecological Restoration, University of California, Santa Barbara, California, U.S.A. and [3]California Toxic Research Institute LLC, San Jose, California, U.S.A.

Abstract. 1. It is hypothesised that ecological restoration in grasslands can induce an alternative stable state shift in vegetation. The change in vegetation influences insect community assemblages and allows for greater functional redundancy in pollination and refuge for native insect species.

2. Insect community assemblages at eight coastal California grassland sites were evaluated. Half of these sites had undergone restoration through active revegetation of native grassland flora and half were non-restored. Insects were collected from *Lupinus bicolor* (Fabaceae) within 2×2-m^2 plots in spring 2017. *Lupinus bicolor* is a common native species that is used in California restoration projects, and home and state landscaping projects.

3. Ordination demonstrated that insect community assemblages were different between restored and non-restored sites. These differences were seen in insect functional groups as well as taxa-specific differences and were found to be driven by environmental characteristics such as non-native forb cover.

4. Functional redundancy of herbivores decreased at restored sites, while pollinators became more redundant compared with non-restored sites. The assemblages of the common species found at restoration sites contained more native insects than those found at non-restored sites, including species such as *Bombus vosnesenskii*.

5. Local grassland restoration has the potential to induce an alternative stable state change and affect insect community assemblages. Additionally, it was found that grassland restoration can be a potential conservation tool to provide refugia for bumblebees (*Bombus*), but additional studies are required to fully understand its broader applicability.

Key words. Alternative stable states, *Bombus vosnesenskii*, ecological restoration, habitat refugia, insect community assemblage, local scale.

Introduction

Land use change causes habitat fragmentation, which is a primary driver of loss of insect biodiversity (Kearns & Inouye, 1997; Letourneau, 1998; Steffan-Dewenter & Tscharntke, 2002; Hendrickx *et al.*, 2007; Dormann *et al.*, 2008). Land use change can include transformation of remnant ecosystems (White & Walker, 1997) to agricultural lands, lawns or community parks, leading to a shift in dominant plant species, plant diversity evenness and a change in ecosystem functions (Vitousek *et al.*, 1997). In such instances, native plant species are displaced by non-native and invasive plant species, which was found to alter insect community assemblages, often decreasing native insect species richness (Litt *et al.*, 2014; Grunzweig *et al.*, 2015).

Ecological restoration (restoration) is a conservation action that involves direct human alteration of an area to improve or ameliorate degraded ecosystem functions, often limited to species richness and composition (Suding, 2011; Kull *et al.*, 2015; Society for Ecological Restoration *et al.*, 2016; Brudvig *et al.*, 2017). Restoration projects vary widely due to habitat type and locality. A common component of many restoration projects is a focus on plant species richness due to correlations between increased species richness and ecosystem functions such as pollination or pest control (Tilman *et al.*, 1996; Loreau *et al.*, 2001; Cardinale *et al.*, 2012; Mace *et al.*, 2012;

Correspondence: Justin C. Luong, Environmental Studies Department, University of California, Santa Cruz, California 95064, U.S.A. E-mail: jluong4@ucsc.edu

Pasari *et al.*, 2013). Other goals of restoration focus on ecosystem services deemed beneficial for humans. For example, forest systems are afforested for carbon sequestration (Silver *et al.*, 2000; Kull *et al.*, 2015) or wetlands for hydrological functions (Jessop *et al.*, 2015). Grassland restoration often attempts to recreate a plant community from a reference site in order to ameliorate plant species richness and loss of evenness (Barak *et al.*, 2017). It is still debated whether grassland restoration through native plant reintroduction can ameliorate loss of insect species richness. However, agroecosystems implementing hedgerows containing a greater species richness of native plants support a more diverse community of native pollinators (Menz *et al.*, 2011; Morandin & Kremen, 2013).

Alternative stable state theory, first proposed by Richard Lewontin in 1969, suggests that a disturbance event or change in habitat (e.g. vegetation composition for insects) will lead to a change in the community composition of the ecosystem, leading to an alternative stable state in the community composition. If another disturbance occurs, there is a chance the community will experience another alternative stable state shift and return to the original community or experience hysteresis, creating a novel community (Beisner *et al.*, 2003). Although restoration aims to restore ecosystems back to an earlier successional community or reference community (White & Walker, 1997), in practice, restoration often induces an alternative stable state shift (Hobbs *et al.*, 2011; Suding, 2011; Brudvig *et al.*, 2017) by creating a novel vegetative community (Lewontin, 1969; May, 1977; Beisner *et al.*, 2003; Suding & Hobbs, 2009; Hobbs *et al.*, 2011). This could potentially allow for recolonisation of the habitat by insects that were previously extirpated (Grunzweig *et al.*, 2015; Watts *et al.*, 2015). For example, a study conducted in Australia found that removal of an invasive plant facilitated an alternative stable state shift, where native beetle species once previously extirpated (locally extinct) recolonised the habitat (Watts *et al.*, 2015). As such, restoration, which often leads to floral diversification in habitats along with the reduction of invasive plant cover (Society for Ecological Restoration *et al.*, 2016), should facilitate a greater persistence of insect diversity (Watts *et al.*, 2015).

The insurance hypothesis predicts that functional redundancy should allow for extirpation of some species without a large effect on ecosystem functioning if those species overlap in function (Yachi & Loreau, 1999; Mouillot *et al.*, 2013), thereby providing the functions and ecosystem services of insects with greater resilience to instantaneous disturbance events as well as long-term change. Functional redundancy is the overlap in the functions that unique species provide in a system; for example, five different bee species with different environmental tolerances allow for greater functional redundancy in pollination than an increased abundance of one or two bee species (Oliver *et al.*, 2015). Although functional redundancy shows promise for increasing the resilience of ecosystem functions provided by insects in restoration projects, most studies have focused on the application of functional redundancy in agroecosystems (e.g. Settle *et al.*, 1996, e.g. Rader *et al.*, 2013, Brudvig, 2017). As such, the insurance hypothesis would predict that functions that overlap in multiple insect taxa would have greater ecological resilience (e.g. Peterson *et al.*, 1998) to disturbance events and environmental change (Yachi & Loreau, 1999; Loreau, 2010; Oliver *et al.*, 2015).

In this study, we compare historic California grasslands in areas that are restored with those that are non-restored. We predicted restoration would induce an alternative stable state shift leading to distinct insect community assemblages between restored and non-restored sites. Furthermore, we predicted that restored sites would have a higher abundance of pollinators due to greater native floral abundance allowing for greater functional group redundancy.

Materials and methods

Lupinus bicolor *species description*

Lupinus bicolor Lindl. (Fabaceae; Sholars and Riggins 2012) is a common annual pea plant found ubiquitously in California, but its range extends into Oregon and Baja California. It occupies a large variety of habitat types, ranging from grassland to chaparral. *Lupinus bicolor* is often used in grassland restoration in California, as well as for state beautification projects along the highway. It was selected as a target species to collect insects because other closely related species within the genus and clade are known to attract a variety of insects (Juncosa & Webster, 2018). Furthermore, although *L. bicolor* is commonly used, little is formally known about its potential as a host plant for insects.

Lupinus bicolor is generally short in stature and pubescent with palmately arranged leaves, but its morphology ranges widely. It has a papilinoid flower with a banner, wing petals and a keel tip that hides the pollination mechanism until it is either landed upon or bored into. Flowers are generally bicoloured, with blue to purple wing petals and a white banner petal often speckled with the colour of the wing petals.

Study area and restoration treatment

This study took place during spring 2017 in a Mediterranean climate, characterised by cool wet winters followed by hot, dry summers with an average rainfall of 35 cm (Mooney & Dunn, 1970), and occasional water input from summer coastal fog. Eight coastal populations of *L. bicolor* were monitored near UC Santa Barbara in Santa Barbara County, California, U.S.A., in order to determine the insect visitors. Within these eight grassland sites, half of the sites were restored, and the other half received no restoration. The eight study sites were at least 2 km away from other sites, but no more than 5 km away from any other site. Restored areas are managed by the Cheadle Center for Biodiversity and Ecological Restoration (CCBER), UC Santa Barbara, and undergo minimal active management in the form of weed control. We intentionally selected restoration sites implemented only by CCBER in order to better control for management differences between restoration groups. Historically, all sites in this study were previously used for agriculture and ranching. Before agricultural use, the land was used as a base for military operations and whaling. Pre-colonial landscapes were suspected to be dominated by grasslands maintained by controlled burns practised by the indigenous Chumash tribe.

During the first 3 years, restored areas received daily work, including weed control, native plant establishment through direct sowing of native seeds and planting of 2-inch pots of native grassland species grown locally. After outplanting, plants were watered once a week for 3 months to help established newly seeded or planted individuals. While planning the restoration projects, remnant coastal grasslands that have been minimally impacted by land use change found within 5 km were used as reference sites (White & Walker, 1997). Plant material used for restoration was restricted by plants found within the local watershed in order to preserve local adaptations and prevent outbreeding depression (Hufford & Mazer, 2003). Focal species used for planting include *Stipa pucha* Hitchc. (Poaceae; Purple Needle Grass), *Bromus carinatus* Hook. & Arn. (Poaceae; California Brome), *Hordeum brachyantherum* Nevski (Poaceae; California barley), *Sisyrinchium bellum* S. Watson (Iridaceae; blue-eyed grass) and *Eschscholzia californica* Cham. (Papervaceae; California poppy). Restoration sites were also directly seeded with annual forbs at the beginning of the rainy season for 2 years with species including *Calandrinia menszeii* (Hook.) Torr. & A. Gray (Portulacaceae Red Maids) and *Salvia columbariae* Benth. (Laminaceae, Western Chia). *Lupinus bicolor* seed was assumed to be latent in the seed bank and was not added to restoration sites. Although planting was a part of restoration, that accounted only for a small portion of actual restoration activity (*c.* 20%).

The dominant restoration management practice used was invasive species removal (*c.* 70%). Although all non-native species were removed when possible, invasive species such as *Avena fatua* L. (Poaceae; wild oats) and *Bromus diandrus* Roth (Poaceae; Rip-gut Brome) with non-native forbs such as *Raphanus sativus* L. (Brassicaceae; wild radish), *Medicago polymorpha* L. (Fabaceae; burclover), *Sonchus spp.* L. (Asteraceae; sow thistles) and *Hirschfieldia incana* (L.) Lagr.-Fossat (Brassicaceae; summer mustard) were high-priority targets. The restoration sites used in this study are no longer being actively restored via native plant re-establishment, but still receive monthly maintenance for invasive plant species control.

At the time of the study, restored sites were dominated by the invasive grass *A. fatua*, but had several native species such as *L. bicolor*, *L. nanus*, *H. brachyantherum* and *C. menszeii*. Non-restored sites are dominated by non-native grasses such as *A. fatua* and *B. diandrus*, and non-native forbs such as *R. sativus* and *H. incana*. Although they have not received any active restoration, these sites were selected because *L. bicolor* had been documented at each site in previous years.

Due to a lack of properly identified specimens and a dearth of local research focusing on insect communities, little is known about the extant insect communities within these habitats other than dominant species such as *Linepithema humile* Mayr (Formicidae; Argentine Ant), and many other non-native insects introduced for agricultural purposes, such as *Apis mellifera* Linneaus, 1758 (Apidae; European Honey Bee) and *Coccinella septempunctata* Linnaeus, 1758 (Coccinellidae; 7-Spot Lady Beetle) with some native insects persisting, such as *Bombus vosnesenskii* Radoszkowsk, *1862* (Apidae; yellow-faced bumblebee).

Lupinus bicolor *visitor observations*

One 2×2-m² plot was demarcated to be regularly monitored. Study sites had non-significant differences in the total number of *L. bicolor* individuals. All insect surveys were conducted by two trained observers twice a week for 30 min per plot; surveys lasted 9 weeks and covered a total of eight sites (four restored sites, four non-restored sites). Each site was sampled with equal sampling effort, totalling 135 h of active observation for each site and 1080 h of active observation in this study. Observation times consisted of observing and collecting visitors solely from *L. bicolor* plants within plots. Diurnal insects are most active during the warmest time of the day, which corresponds with peaks in flower nectar resources. Because of this, observations occurred between 10.00 and 16.00 hours, in order to cover the greatest potential suite of insects visiting *L. bicolor* (Herrera, 1990). In addition, one set of early and one of late sampling (beginning at 08.00 and 17.00 hours) were conducted to increase the likelihood of including temporal niche visitors.

At each plot, data were collected regarding local weather conditions and insect interactions relating to *L. bicolor*. Sampling methods included nets, aspiration, beating, hand collection and flower collection for dissection. Most samples were collected through aspiration and by hand, with nets utilised as necessary to minimise damage to the plants. Beat sampling, which allows for collection of potential specimens that could be hiding in flowers (i.e. beetles or thrips), was conducted on every *L. bicolor* individual in the plot during each observation period. Flower samples were carefully dissected and any specimen found within the flower was placed in 70% ethanol. Specimen collection was in compliance with California state and federal laws and samples were vouchered at the Invertebrate Zoology Collection at CCBER (specimen accession codes: UCSB-IZC00024640–UCSB-IZC00024960).

Specimens were identified to species using a dichotomous key whenever possible (Carvalho, 1955; Slater & Baranowski, 1978; Schuh & Slater, 1995; Gibson *et al.*, 1997; Arnett *et al.*, 2002; Gordon, 2009; Daniel & Franz, 2012; Hoddle *et al.*, 2012; Marshall, 2012). Specimens that could not be identified to species were determined to putative species or morphospecies for analyses (see Supporting information, Table S1; Samways *et al.*, 2010).

Site characterisation

The total number of *L. bicolor* plants was determined at each site, and sites were selected so that the total individual number of *L. bicolor* plants did not vary significantly. In addition, two 8-m transects were placed perpendicular to each other in the centroid of each plot. Absolute plant ground cover was measured to the nearest percentage using a 1×1-m quadrat along alternating sides of the transect belt at each metre during the peak flowering season in order to characterise the baseline plant species absolute cover and species richness. Species richness was used as a metric of plant diversity.

During the second week of the study (8 April 2016), all study sites were surveyed to determine their environmental characteristics. Parameters quantified included the percentage of

plants that are grass, shrub or tree; the percentage of ground that is vegetated or bare; and the total abundance of *L. bicolor*.

Statistical analyses

All analyses were completed in R statistical software v.3.5.1 (R Core Team, 2018). Tests for normality found that all data used in parametric analyses fitted a normal distribution. Parametric two-way ANOVA was used to determine differences between the total abundance of specimens from each feeding guild: abundance within guild × feeding guild class, abundance within guild × restoration treatment, and abundance within guild × feeding guild class:restoration.

Dissimilarity analyses were used to assess differences in insect community assemblages and were completed using the VEGAN package in R (Oksanen *et al.*, 2018). Bray–Curtis dissimilarity indices were generated in order to quantify the compositional dissimilarity between two different sites (restored and non-restored) based on insect abundance observations at each site (Beals, 1984). Bray–Curtis was selected because it can handle community matrices with many zeros, which can often cause zero-inflation-related issues in other dissimilarity indices.

Community composition was visualised through non-metric dimensional scaling ordination (NMDS). Environmental variables matrices were then created by averaging site environmental field data (Table S2), and these were tested for correlation among themselves using Pearson's correlation via the CORRPLOT package in R (Wei *et al.*, 2017); this test is considered ideal, as environmental variables are continuous. We subsequently ran a permutational multivariate analysis of variance (PERMANOVA), running the environmental matrix against the community data (derived from the total abundance of each morphotype at each site; Table S1) to determine environmental characteristics key in distinguishing communities (e.g. Fig. 2). After initial analysis, for any environmental variables that were correlated to each other using the Pearson test, only the variables with the strongest effect in the initial PERMANOVA were retained to improve statistical power. Using a canonical correspondence analysis, we were able to determine the degree of variation explained by fitted environmental variables.

Rank abundance plots (Whittaker plots; Fig. 3) were used to compare ranked species distribution and diversity (Whittaker, 1965) and were created using the BIODIVERSITYR package, visualised using GGPLOT2 (Kindt, 2018; Wickham *et al.*, 2018). Shannon diversity indices were calculated using BIPARTITE (Dormann *et al.*, 2018).

Results

Insect community assemblages

The community compositions of insects found within restored and non-restored sites were slightly overlapping, but they were different in many aspects, as seen by their partially overlapping polygons (NMDS; $k = 3$, stress $= 0.0482$; Fig. 2). Bare ground cover was correlated with non-native forb cover ($r = 0.80$, $P < 0.05$; Fig. 1), and non-native plant cover was correlated with
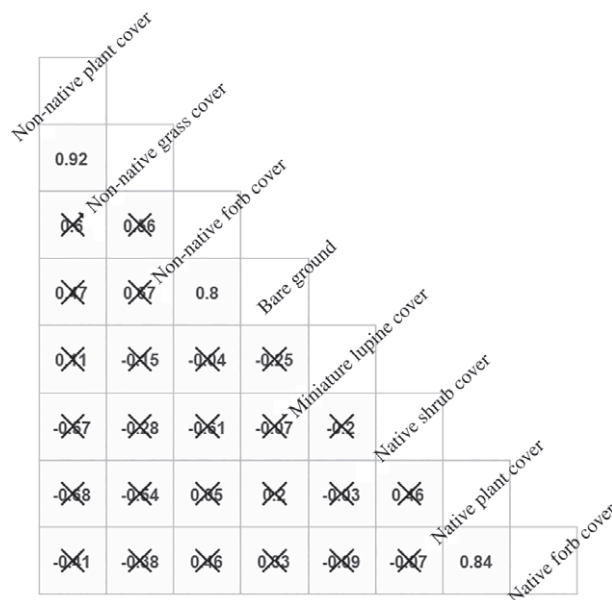

Fig. 1. Pearson's correlation matrix. Crossed-out values are non-nsignificant, and unobscured values are significant ($P < 0.05$). Scale ranges from 1 to −1, representing complete direct correlation to complete inverse correlation.

non-native grass cover (Pearson's $r = 0.92$, $P < 0.01$), indicating that non-native grasses play a greater role in shaping insect communities within non-native plants compared with other non-native plant life forms. Native forb cover was correlated with overall native plant cover, similarly indicating that trends from overall native plant cover are driven more by native forbs than by other native plant life forms ($r = 0.84$, $P < 0.01$).

The restored sites had greater ground cover of native shrubs and *L. bicolor* (Fig. 2). Insect assemblages within non-restored sites were found to be slightly overlapping with restored sites. As none of these areas have had *L. bicolor* seed intentionally introduced as a restoration treatment, we found that the abundance quantified by the total number of individuals of *L. bicolor* between sites did not vary significantly ($P > 0.05$) and that the absolute ground cover of *L. bicolor* was a significant environmental variable in structuring and distinguishing insect communities between restored and non-restored sites (PERMANOVA: $R^2 = 0.23$, $P < 0.01$), whereas the cover of non-native forbs approached significance, but ultimately did not play a significant role ($R^2 = 0.18$, $P = 0.09$). This also indicates that, although the total number of *L. bicolor* individuals did not vary between restored and non-restored sites, the maximum ground cover was larger (individuals were larger) in restoration areas.

Differences in community functional groups

In order to better understand distribution of insect functional groups between restored and non-restored sites, we summed the abundances of each feeding guild from each site (Fig. 3). Thereafter, those sums were averaged to determine the average abundance of specimens collected from each
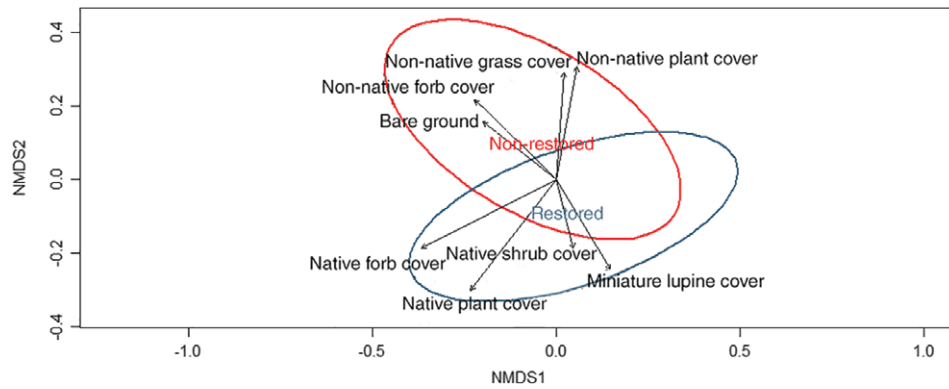
Fig. 2. Non-metric dimensional scaling (NMDS) plot visualising the relative differences and similarities in insect community assemblages within restored and non-restored sites. Each bubble represents the differences in species abundance and evenness of insects collected. Environmental fitted vectors are mapped on the NMDS. These vectors represent environmental variables that are useful in distinguishing why differences between communities arise. [Colour figure can be viewed at wileyonlinelibrary.com].

feeding guild by treatment. We found that there were nearly significant differences in abundance within guild × restoration treatments ($F = 3.53$, d.f. $= 1$, $P = 0.07$). Differences were found between abundance within guild × feeding guild class ($F = 10.0$, d.f. $= 4$, $P < 0.0001$); however, we found no significant interaction between abundance within guild × insect feeding guild class:restoration treatment ($F = 1.78$, d.f. $= 4$, $P = 0.17$). Tukey *post hoc* analyses revealed that herbivores dominated non-restored sites ($p_{adj} < 0.01$), with significantly greater abundance compared with nectivores, decomposers, predators and parasitoids. Within restored sites, herbivores were dominant, but to a lesser degree, there were no significant differences in the abundance of herbivores and decomposers ($p_{adj} = 0.32$), as well as nectivores ($p_{adj} = 0.67$), and there was only dominance over predatory and parasitoid insects ($p_{adj} < 0.05$).

Species-specific differences

Using rank abundance plots, we were able to visualise and compare the differences between taxa collected within restored and non-restored sites (Fig. 4). The overall slope of the rank abundance curve indicates that the Shannon diversity index (H') at restored sites is 3.842, which is greater than at non-restored sites where the H' was found to be 3.422. These plots (Fig. 4) indicate the alpha diversity or total species richness collected from different collection areas. Alpha diversity within restored sites was found to be $\alpha = 64$, which is comparable with non-restored sites where alpha diversity was found to be $\alpha = 65$. As alpha diversity did not vary much between sites, it can be inferred that the higher H' within restored sites was due to a higher level of species evenness.

The main contrasting point between restored and non-restored sites in our observations was that *Bombus vosnesenskii*, a native bumblebee and pollinator, was the most common species in restored sites whereas they do not even rank in the top 15 in non-restored sites. The top five species found in restored sites were *B. vosnesenskii* (nectivore), *A. mellifera* (nectivore),

a morphospecies from the tribe Paralimnini (Cicadellidae; herbivore), a morphospecies from Heleomyzidae (decomposer) and *Coccinella septempunctata* (predator). *Thrips* sp. Linnaeus (Thirpidae; herbivore), *Ceratagallia californica* (Baker, 1898) (Cicadellidae; herbivore), *C. septempunctata* (predator), *A. mellifera* (nectivore) and a morphospecies from Heleomyzidae (decomposer) were the most common species in non-restored sites (Fig. 4).

Discussion

Our results suggest that local scale native plant restoration has the potential to induce an alternative stable state shift as the composition of the vegetation community is altered. Restoration reparations can result in the formation of unique insect community assemblages within restored grasslands (Figs 2–4). Furthermore, we found that restoration has the potential to increase evenness between functional groups of insects (Fig. 3); specifically, increasing functions such as pollination and decomposition while decreasing herbivory, which is especially important as dominance of any functional group has been found to decrease overall ecosystem functions (Winfree *et al.*, 2018). Changes in insect functional groups can be linked to taxa-specific changes between restored and non-restored sites (Fig. 4).

Our study is one of the first to delve into the potential of local scale restoration to shape insect community assemblages outside of agricultural systems. In particular, we found that the relative ground cover of *L. bicolor*, native and non-native forbs versus other plant life forms was the most important site characteristic in distinguishing local insect community assemblages. Forbs are non-woody herbaceous flowering plants, not including gramminoid (grass, rush, and sedge) life forms. The cover of a specific native forb, *L. bicolor*, was found to be more strongly associated with restored sites, whereas non-native forb cover was associated more with non-restored sites. Although it may seem obvious that restoration will affect plant communities, many studies have found that restoration is often unsuccessful and can revert to the starting conditions
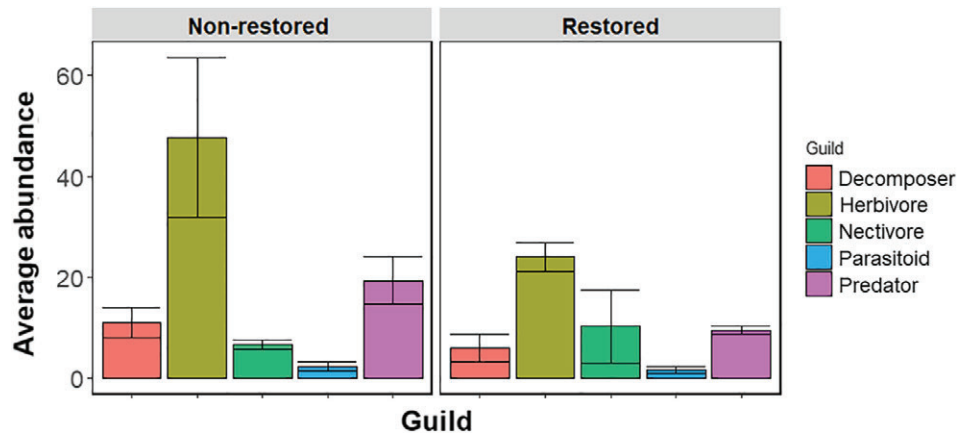
Fig. 3. Plots show the mean abundance of feeding guilds of insects collected by site. Non-restored sites were dominated by herbivorous insects relative to any other feeding guild ($p_{adj} < 0.01$). Restored sites were also dominated by herbivores, but to a lesser degree, showing greater abundance only over predators and parasitoids. [Colour figure can be viewed at wileyonlinelibrary.com].
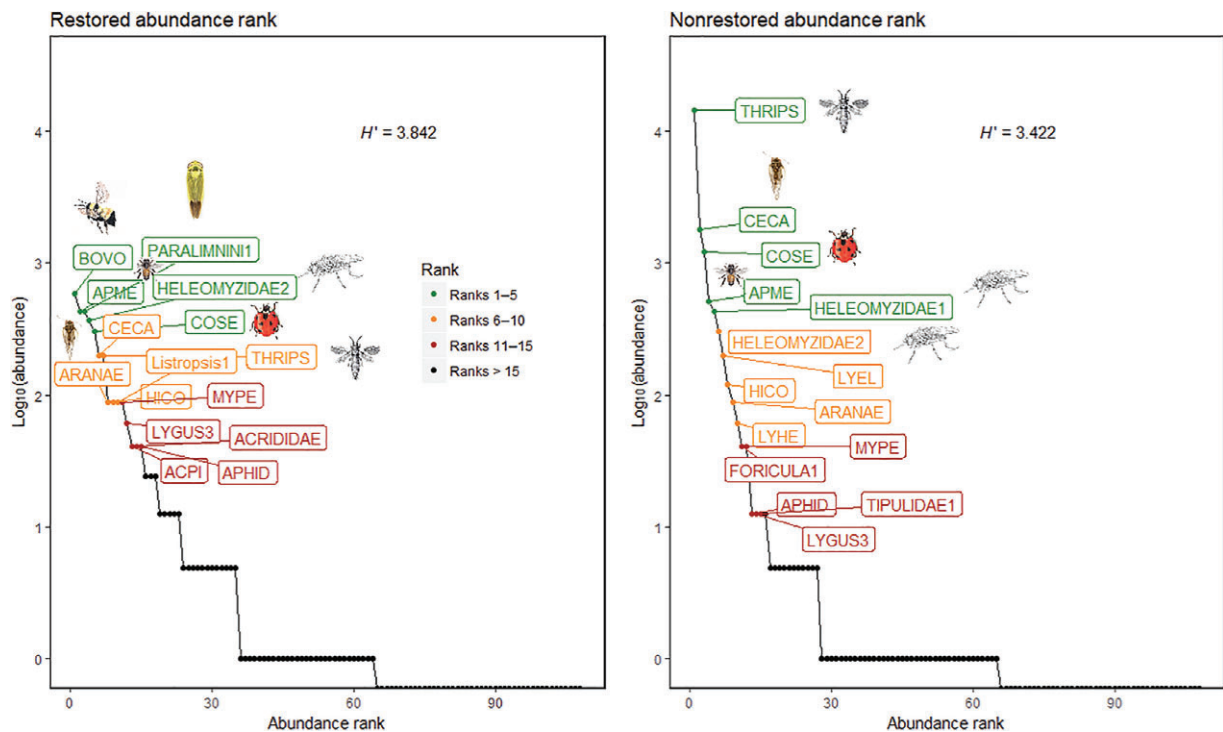

Fig. 4. Rank abundance plots. The total length of the *x*-axis represents total species richness, whereas the distance between two points represents relative evenness. Top ranks (1–5) are in green, ranks 6–10 in are yellow, and ranks 11–15 are red. Species lower than 15 in abundance rank were not labelled. The key differences are that the restored sites had a greater number of beneficial species than did non-restored sites. The most common species in restored sites was *Bombus vosnesenskii*, a native bumblebee, and the most common species in non-restored sties was *Thrips*, a common plant pest. [Colour figure can be viewed at wileyonlinelibrary.com].

without continued intervention (Suding & Hobbs, 2009; Suding, 2011; Brudvig *et al.*, 2017). In a previous study, Watts *et al.* (2015) found that removal of non-native plants led to an alternative stable state shift, leading to distinct changes in the insect community; in another study, Grunzweig *et al.* (2015) found that an invasive plant rendered the habitat unsuitable for many of the local insects. Similarly, in our study, the gradient

of change in the forb and *L. bicolor* cover could indicate an alternative stable state shift (Beisner *et al.*, 2003).

In particular, we found that the change in the forb community induced by restoration decreased the dominance of herbivorous insects (Fig. 3). This finding supports the theory that restoration can induce an alternative stable state shift by bringing the habitat closer to a reference site's state before plant invasion. This

shift closer to the reference site is supported by a meta-analysis which found that invasive plants often increase the abundance of herbivorous insects (Litt *et al.*, 2014). Alternatively, as environmental change occurs and plant invasion affects biological interactions, hysteresis could occur in the local system, causing the state shift not to come closer to the reference system and become a novel system (Beisner *et al.*, 2003).

Within restored sites, herbivores only had dominance over parasitoids and predators, as opposed to non-restored sites where herbivorous insects also had dominance over decomposers and nectivores. From this we can infer that the dominance of herbivores is decreasing in restored sites. Furthermore, because there are non-significant differences in species richness between restoration treatments (64 in restored, 65 in non-restored), and because non-restored sites are dominated by herbivores, we can infer that the functional redundancy of functions such as pollination and nutrient cycling (nectivores and decomposers) is higher in restored sites. In the rank abundance plot (Fig. 4), we can also see the specific taxa differences driving the functional differences in the system.

The dominance of herbivores in non-restored sites was caused by variation in the abundance of *Thrips* spp. (a commonly known plant pest; Morse & Hoddle 2006) and *Ceratagallia californica*, whereas restored sites were less dominant in *Thrips* spp. (it was the sixth most common species), probably causing an increase in the diversity index at restored sites (Fig. 4). *Thrips* spp. are often considered undesirable for plant restoration (Leong & Bailey, 2000), as they can adversely affect native plant establishment. For similar reasons, the spread of *Thrips* spp. outside of restoration areas to surrounding areas is undesirable for local landowners and managers, especially in agricultural and garden productions (Morse & Hoddle, 2006). Instead, herbivores at the restored sites were dominated by the native leafhoppers *C. californica* and a morphospecies from the tribe Paralimnini, which are often used as indicators of good-quality grassland habitat (Hollier *et al.*, 2005; Nemec & Bragg, 2008).

Bombus vosnesenskii was the most common specimen collected at restored sites, whereas it was uncommon at non-restored sites. *Apis mellifera* was common at both sites, indicating that restored sites had greater functional redundancy in pollination. Although it was outside the scope of this study, this could also indicate greater pollination services provided at restored sites, as *A. mellifera* is known to partake in nectar larceny (Dedej & Delaplane, 2005), circumventing pollination and decreasing the chances of the plant being pollinated by another insect due to reduced levels of available nectar (Inouye, 1980). Furthermore, as bumblebees are known to be in decline (Goulson *et al.*, 2008) and were found to be common in restored sites, our results indicate that grassland restoration is potentially a valuable conservation tool for providing refuges for bumblebees in California.

As the goal of our study was to elucidate patterns with insect communities and small-scale restoration, our results may not be applicable at a larger scale. We also focused on the coastal area, because human populations are concentrated in these areas and have the potential to experience more adverse anthropogenic effects (Vitousek *et al.*, 1997). Accordingly, we recommend that future studies focus on a wider geographic range of small-scale

grassland restoration projects or on specific insect families or groups. In particular, community surveys targeting the abundance of bumblebees and other native bees in restored and non-restored grasslands can further discriminate whether or not grassland restoration is an effective conservation tool for bumblebees and whether or not it is applicable at larger scales. This is particularly important, as coastal California grasslands are classified as an endangered habitat and may function differently from other grasslands. Additionally, our study only encompasses the restoration activities of one particular restoration group, the CCBER, and it will be important for future studies to incorporate areas restored by additional groups to determine the role of specific management practices.

Conclusions

Disturbance events leading to the establishment of invasive plants and an alternative stable state shift (Holling, 1973; Litt *et al.*, 2014; Grunzweig *et al.*, 2015) in the local plant community subsequently alter insect community assemblages, often decreasing local insect species richness (Watts *et al.*, 2015). However, our results demonstrate that restoration can induce another stable state shift, bringing the system to a new alternative state that is not identical to reference systems or non-restored sites (Beisner *et al.*, 2003). Our results further demonstrate that distinct changes within insect assemblages can be observed within native plant restoration at a local scale, which has rarely been documented (Hubbell & Johnson, 1975; Conner & Neumeier, 1995). In addition to testing the applicability of stable state theory in restoration (Wainwright *et al.*, 2017), our results also have management implications showing that restoration has the potential to decrease the functional dominance of herbivores and taxon dominance. Dominance in habitats is important, as it is one of the few factors known to be detrimental to ecosystem services and to scale up spatially (Winfree *et al.*, 2018). Specifically, local grassland restoration can be implemented as a technique to provide local-scale refugia for native bumblebees in coastal California.

Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1. Collection of specimens from each of the sites.

Table S2. Corresponding environmental characteristics for each of the sites from which specimens were collected.

References

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