Characteristics of plant communities invaded by *Dittrichia graveolens* (Asteraceae), as it spreads away from roadsides in Santa Clara County

Andrew Lopez

Undergraduate Thesis

Department of Ecology and Evolutionary Biology

University of California, Santa Cruz

Advisor: Ingrid M. Parker

13 March 2021

Abstract

Plant invasions are often facilitated by transport corridors due to high levels of bare ground and low species diversity. Some introduced plants are restricted to these disturbed environments, while others are able to spread away from corridors and become invasive. Understanding the factors that contribute to this invasion process can help direct time and money more effectively. *Dittrichia graveolens* (L.) Greuter is an annual plant in the Asteraceae family native to the Mediterranean region. *Dittrichia* was first observed in California in the 1980's and is often found growing along roadsides and in disturbed soils. Since its introduction, *Dittrichia* has spread across the state and has now invaded about three-quarters of California counties. More recently, the species has been observed spreading away from roadsides and into natural habitat off-road. We hypothesized *Dittrichia* invasion would be highest in disturbed sites off-road, but would be limited in more diverse communities. We surveyed 15 population pairs in Santa Clara County by selecting *Dittrichia* populations from off-road sites, with each being paired to the nearest roadside site, which we presumed to be the most likely source of *Dittrichia* invasion. Using quadrats, we measured percent cover of *Dittrichia*, other vegetation, and bare ground, and estimated species diversity within the *Dittrichia* population. We predicted that away from roads, *Dittrichia* populations would be larger in more disturbed sites and that *Dittrichia* cover would be lower in more diverse plots. We found that these predictions were not supported. Roadside sites had greater percent cover of bare ground, while percent cover of other vegetation and alpha diversity were similar for roadside and off-road sites. Population size was larger in roadside sites, although percent cover *Dittrichia* was significantly higher for off-road sites. Interestingly, disturbance only significantly predicted *Dittrichia* density at the quadrat level. Lastly, species richness was a poor predictor of *Dittrichia* density and population size for off-road sites. We suspect that environmental factors that increase species diversity may also favor *Dittrichia*

invasion. These results provide implications for protecting habitat with high conservation value and may offer insight for directing resources when managing *Dittrichia.*

Introduction

Biological invasions occur when exotic species move into and establish populations in new regions, often with adverse consequences for native species, communities, and ecosystems (Simberloff 2010; Shabani et al. 2020; Yan et al. 2020). Plant invasions have three phases: introduction, colonization, and naturalization (Radosevich et al. 2003). The introduction phase may be hard to detect and often depends on environmental factors that provide a suitable habitat. Colonization occurs as the species range expands, which involves biological traits such as seed dispersal mechanisms. During naturalization, expansion slows and the invading species is integrated into the community. Invasive species, by definition, are found outside captivity and may exist as a self-sustaining population, and it has been estimated that only 1% of a single introduced species will become established and pose a threat (Williamson and Fitter 1996).

The spread of invasive plants is often facilitated by transport corridors such as roads and railways (Tyser and Worley 1992; Gelbard and Belnap 2003; Hansen and Clevenger 2005; Christen and Matlack 2006), but the processes by which invasive plants spread away from corridors are poorly understood (Ward et al. 2020). Roadside habitats are characterized by high levels of disturbance and lower diversity, both of which may facilitate invasion. Disturbance in general is an event that causes disruption to an ecosystem, community, or the structure of a population, leading to shifts in resources and the physical environment (Luisa 2012). Along roadsides, disturbance may result from human activities such as trampling or mowing, but other events like grazing from animals, wind damage, fire, and soil erosion also constitute disturbance (Grime 1974; Grime 1977). The impacts of these events on plant communities are highly variable and depend on factors like environmental conditions, the primary strategies of species, and the level of disturbance (Connell 1978; Hughes et al. 2007; Mackey and Currie 2016). Despite variable impacts, predictions may be made by understanding the primary strategy for a species. Ruderal species are able to colonize disturbed habitat, and most have a short life cycle with the ability to produce many seeds that germinate rapidly under disturbance events (Frenkel 1977; Grime 1977). Many invasive plant species show the traits of ruderal species and successful colonizers (Baker 1965).

The potential for invasive species to spread and establish away from roadsides depends on many factors, some of which include the dispersal range and habitat specificity of the invader, and the existing vegetation and disturbance of the habitat (Gelbard and Belnap 2003; Christen and Matlack 2006). The concept of biotic resistance refers to the ability of species in a community to resist or limit invasion by exotic species, and factors like competition and diversity often contribute to resistance (Byers and Noonburg 2003; Levine et al. 2004; Beaury et al. 2020). Although there is evidence that communities lacking diversity are more susceptible to invasion, it has also been suggested that communities with more diversity may also be at risk. Research suggests that such communities are often linked with an increase in resources (Huston and Huston 1994; Rejmánek 1996), and may be especially vulnerable to invasion with additional management challenges (Stohlgren et al. 1998; Stohlgren et al. 1999).

Invasion away from roadsides may also impact agriculture and in such cases the invader competes with and reduces the value of food crops, posing great concern to farmers (Westbrooks 1998; Schroeder et al. 2005). Early detection and rapid response are crucial steps in preventing the spread of invasive species (Simberloff 2003), and this approach aims at eradicating invaders before they become established (Westbrooks 2004). This method of control against invasive species should be of high priority to ensure that the impacts of invasion are limited and not posing a risk to agriculture or species rich native habitat.

A recent California invader, *Dittrichia graveolens* (L.) Greuter, is an annual plant native to the Mediterranean region and was first reported in Santa Clara County in 1984 (Preston 1997). It grows in disturbed soils and in riparian woodlands, marshes, vernal pools, and other wildland areas. Although native to the Mediterranean Basin region of Europe, *Dittrichia* is invasive in other parts of the world including Australia and the United States. In California, *Dittrichia* has been dispersing from a presumed epicenter of Santa Clara County (Brownsey et al. 2013a) and is now found in more than three-quarters of California's counties (Fig. 1). Its range spans the northern and southern portions of the state and is moving eastward into the foothills of the Sierra Nevada Mountains. *Dittrichia* first establishes along roads and disturbed areas, then into adjacent natural sites off-road.

The goal of this research is to examine factors affecting populations of *Dittrichia* as they invade off-road sites and to characterize invasible sites. I test three hypotheses: 1) roadside sites have more individuals and greater percent cover of *Dittrichia*; 2) off-road sites with more bare ground have larger and more dense populations of *Dittrichia*; and 3) more diverse off-road communities have smaller populations with lower cover of *Dittrichia*. Thirty *Dittrichia* populations from fifteen paired roadside and adjacent off-road sites were sampled throughout Santa Clara County. We seek to provide insight into the factors that facilitate invasion away from roads by focusing on disturbance and biodiversity in off-road sites.

Materials and Methods

Natural History

Dittrichia is a late-season annual that produces yellow flowers in the early fall and sets seeds from September through December. A single large plant is capable of producing up to 25,000 seeds with estimated viability of 90% (Brownsey et al. 2013b). The seeds have barbed hairs and pappus, allowing them to be dispersed by wind, machinery, animals, and other vectors.

Locality and Field Sites

All locations were in Santa Clara County, within a 20-mile radius of Alviso, CA (Fig. 2). Surveys began June 19, 2020 and ended August 11, 2020. At each location, we found one pair of roadside and off-road sites. Sites were selected by finding a roadside population of *Dittrichia* with at least 10 individuals growing along roads used by vehicles, but not roads inside a park where only service vehicles are allowed. We then located the nearest off-road population of at least 10 individuals by moving away from the road into more natural habitat. We located 15 pairs of roadside and off-road populations for this project (Fig. 3).

Field Methods

Latitude, longitude, and elevation were collected at each population using a compass application on a cell phone (Table 1). At each site, we walked around the perimeter of the *Dittrichia* population, noting shape and marking its boundary with flagging tape or large rocks at multiple points. We laid a 50m tape as a transect along the longest axis to ensure sampling the entire population. To estimate the size of each *Dittrichia* population, we counted the number of individuals on one side of the transect out to the perimeter, and doubled that number. The outcome of this estimate was placed in one of our predetermined population size categories (10; 50; 100; 500; 1,000; 10,000+).

We placed a 0.5 x 0.5m quadrat at three equidistant points along the axis (Fig. 4). Percent cover was visually estimated for *Dittrichia*, other vegetation, and bare ground inside each quadrat. Gloves were worn to protect skin from allergic contact dermatitis when handling *Dittrichia* and any materials in contact with *Dittrichia*. Other plants growing within the quadrats and boundaries of the *Dittrichia* population were identified to species, when possible. Plants that could not be identified in the field were sampled for later identification using keys in The Jepson Manual: Vascular Plants of California (Second Edition).

Data Analysis

Population size of roadside and off-road sites was compared using a paired t-test (N=15 pairs). Mean population level percent cover of *Dittrichia*, bare ground, and other vegetation in roadside and off-road sites were compared using a paired t-test (N=15). Quadrat level alpha diversity was compared between roadside and off-road populations using a paired t-test (N=15). I used regression analysis to explore the effects of disturbance (% cover bare ground) and diversity (number of species) on population size (number of individuals) and density (% cover) of *Dittrichia*. For these regressions, there were three quadrats (replicates) per site with 15 sites total (N=45). JMP Pro 15 was used for all paired t-tests and regression analyses.

We used a multivariate analysis to characterize sites invaded by *Dittrichia* and to explore how plant community composition was related to *Dittrichia* invasion. Ordination of plots was done with a Principal Coordinates Analysis using a presence/absence matrix of plots and species, without including *Dittrichia* in the dataset (R package ecodist; Goslee and Urban 2007). We eliminated rare species that were only found in 1 or 2 plots. *Dittrichia* abundance (population size) was then layered on top of the analysis for inspection, showing the size of the *Dittrichia* population for each of the sites.

Results

Site Characteristics

Roadside sites had higher percent cover of bare ground than off-road sites (Fig. 5, df = 14, paired t = 3.01, P = 0.009), while percent cover of other vegetation was not detectably different between roadside and off-road sites (Fig. 6, df = 14, paired t = 1.45, P = 0.170). Alpha diversity inside the $0.25m^2$ quadrats ranged from 1 to 7 species and was similar for roadside and off-road populations (Fig. 7, df = 14, paired t = 0.69, P = 0.499).

Population Size

Contrary to our prediction, roadside populations were not larger than off-road populations (paired $t = 1.37$, $df = 14$, $P = 0.191$). In fact, there was a non-significant trend toward larger populations off roads (Fig. 8).

Percent Cover Dittrichia

Average population level *Dittrichia* cover never exceeded 50%. Mean percent cover *Dittrichia* was higher in off-road populations than roadside populations (Fig. 9, paired $t = 3.58$, $df = 14$, $P = 0.003$)

Disturbance

The relationship between degree of disturbance (% cover bare ground) and density (% cover) of *Dittrichia* at the quadrat scale was significant with a negative trend (Fig. 10, *Dittrichia* density = 28.66 - 0.2484 * (disturbance), $N = 45$, $P = 0.012$, $R^2 = 0.138$), while mean disturbance did not significantly predict mean *Dittrichia* density at the population level (Fig. 11, *Dittrichia* density = 26.69-0.1996 * (disturbance), $N = 15$, $P = 0.182$, $R^2 = 0.133$).

The degree of disturbance was a poor predictor for *Dittrichia* total population size in off-road sites (Fig. 12, log10 * (population size) = 2.84 + 0.0033 * (disturbance), $N = 15$, $P = 0.590$, $R^2 = 0.023$).

Diversity and Composition

The relationship at the quadrat level between *Dittrichia* density and alpha diversity (number of species) in off-road populations was not significant (Fig. 13, *Dittrichia* density = 26.38 - 2.29 * (alpha diversity), N = 45, P = 0.19, R^2 = 0.039), nor was it significant at the population level (Fig. 14, *Dittrichia* density = 12.01 + 0.52 * (alpha diversity), N = 15, P = 0.390, R^2 = 0.059).

In off-road sites, alpha diversity was a poor predictor for *Dittrichia* population size (Fig. 15, log10 * (population size) = 2.664 + 0.022 * (alpha diversity), N = 15, P = 0.365, R^2 = 0.063).

Overall, we identified 47 species across our sites, including representatives of the Asteraceae, Poaceae, Verbenaceae, Fabaceae, Plantaginaceae, and Amaranthaceae (Appendix A). Principal Coordinates Analysis was used to study variation in plant composition on roadsides and in off-road sites, and how it relates to *Dittrichia* invasion (Fig. 16). Axis 1 explains 22% of variance and axis 2 explains 17% of variance. *Carduus pycnocephalus*, *Baccharis pilularis, Anagallis arvensis, Polypogon monspeliensis*, *Cirsium vulgare*, *Gnaphalium palustre*, and *Erodium cicutarium* contributed significantly to Axis 1, with plots at the low end of Axis 1 showing fewer Asteraceae species compared to plots at the high end of Axis 1. *Avena*, *Centaurea solstitialis*, *Lepidium*, and *Amaranthus* contributed significantly to Axis 2; plots on the high end of Axis 2 were composed of Poaceae species. As shown by the size of circles in Figure 16, *Dittrichia* associated more with other Asteraceae species, and less frequently with annual grasses, such as *Avena*. The largest *Dittrichia* populations were found in locations that had less *Avena.*

Discussion

As we predicted, roadside sites had greater percent cover of bare ground. Interestingly, we found that percent cover of other vegetation and alpha diversity were both similar between roadside and off-road sites. This contradicts our initial expectation that off-road sites would have greater percent cover of vegetation, while also having greater species diversity. It was presumed that off-road habitat would be less disturbed by humans and therefore we would observe higher vegetation density and an increase in species diversity when compared to roadside sites. Although the latter results do not align with our prediction, we were not surprised to find that roadside sites had more bare ground. The roadside sites surveyed in this study were located near major roads and often appeared to be disturbed by human activity such as mowing, construction, and vehicle traffic, all of which may be linked to an increase in bare ground.

Contrary to what we hypothesized, roadside populations were not larger than off-road populations and had significantly lower *Dittrichia* cover than adjacent off-road populations. In fact, we noted a non-significant trend toward larger populations off-road. *Dittrichia* spreads rapidly along transport corridors, thus we expected to see larger populations with more individuals along roads. Roads often act as corridors for invasion, provide suitable habitat for invasive species, and may act as reservoirs for future invasion events (Parendes and Jones 2000) and it is likely *Dittrichia* is following this pattern. Invasion away from roads and into natural habitat remains poorly understood, yet the non-significant trend of larger off-road *Dittrichia* populations indicates this may be an area of great concern. Stohlgren et al. (2003) proposed the theory of biotic acceptance, in which they suggested that native species richness increases with habitat quality, so we would observe greater species richness in good habitat. Moreover, it was suggested that good habitat is also generally favored by exotic species (Stohlgren et al. 2003;

Fridley et al. 2007). When considering off-road sites in this study, the significantly higher percent cover of *Dittrichia* and non-significant trend of larger populations support the theory of biotic acceptance and put forth the idea that off-road habitat is more favorable for both native and exotic species. Given that *Dittrichia* is still a recent invader in California, these results suggest that primary invasion is continuing to expand along roads while secondary invasion into off-road habitat is increasing as a consequence.

At the quadrat level, disturbance in off-road sites was significantly negatively related to *Dittrichia* density, while mean disturbance was not significantly related to *Dittrichia* density at the population level for the same off-road sites. In addition, disturbance was a poor predictor of population size for off-road sites. Percent cover *Dittrichia*, other vegetation, and bare ground was visually estimated using a $0.25m^2$ quadrat at three points for each population. Because all types of cover sum to one, we expected to observe a negative trend between *Dittrichia* density and bare ground for the quadrat level analysis, although it was interesting to find no significant relationship for density and population size with disturbance at the population level. These results refute our hypothesis that off-road populations with more bare ground would have larger populations with greater *Dittrichia* density. We expected to observe a positive trend between both population size and density with disturbance given that *Dittrichia* is often observed growing in disturbed areas in California (Brownsey et al. 2014), yet our results suggest that disturbance may not be a major factor facilitating *Dittrichia* invasion in off-road habitat. Although supporting evidence reveals that invasion by ruderal species is influenced by disturbance, it is important to acknowledge that disturbance events are often followed by increases in resource availability (Chytrý et al. 2008). I suspect that invasion into off-road habitat still poses risks in the case that resources are readily available even when disturbance events do not occur. This presents concerns regarding the risk of invasion into undisturbed off-road sites of high conservation value.

Dittrichia density was not predicted by species richness in off-road sites at the quadrat level nor the population level. Species richness was also a poor predictor of population size in off-road sites. These results do not support the hypothesis that more diverse off-road sites would be better able to resist *Dittrichia* invasion through biotic resistance and hence would have smaller populations with lower *Dittrichia* cover. Instead, time since introduction and climate may be better predictors of *Dittrichia* population size and cover in off-road sites. In California, it has been found that both of these factors are associated with population size for *Centaurea solstitialis*, a highly invasive plant in North America (Braasch et al. 2019). Moreover, time since introduction was the most significant predictor of non-native range size in marine invertebrates (Byers et al. 2015), suggesting that such a factor is ubiquitous across kingdoms. To further understand how this relates to *Dittrichia*, one could focus on new populations to collect data on climate, spread, and population size over a long period of time (10+ years). I would expect that populations would increase in size and expand their range, but I expect that range expansion may be limited to areas with climate that is representative of the native range for *Dittrichia*.

Our multivariate analysis suggested that our sites grouped into sites with high amounts of exotic grasses (e.g., *Avena, Bromus*) and other sites with more bare ground and more forbs, including Asteraceae. *Dittrichia* tended to associate more with other Asteraceae species than annual grasses. The largest *Dittrichia* populations were in locations with fewer annual grasses, which is consistent with the previous conclusion that more diverse off-road sites have a non-significant trend of higher *Dittrichia* cover. From field observations, the annual grasses in these sites tended to grow at high density, and it appears that grassland sites strongly dominated by annual grasses may be better able to resist *Dittrichia* invasion. Competition may impact invasion success (Goldstein and Suding 2014), and when other invaders have already established there may be limitations imposed on the introduction of new species (Levine et al. 2003). In California, *Avena* is a winter annual that tends to flower from March to June, while *Dittrichia* is a late season annual that flowers from September to December. It has been recorded that *Avena barbata* can limit the establishment of native species by exhausting resources like water and nutrients (Standish et al. 2008). I suspect that early season annual grasses like *Avena* are able to outcompete late season invaders like *Dittrichia* by exhausting available resources, which limits establishment in areas with a high density of such grasses.

To better understand factors that influence *Dittrichia* invasion into off-road sites, one could do an experiment in which disturbance is manipulated, for example by tilling the soil and removing or reducing existing vegetation. Such an experiment for *Dittrichia* is underway at Blue Oak Ranch Reserve. Our prediction is that as disturbance (bare ground) increases, *Dittrichia* will perform better. As competition increases (bare ground decreases) individuals from off-road sites may show an evolutionary competitive advantage compared to individuals originating from the roadside. My observational results on disturbance suggest that the experiment may show disturbance does not predict the size and cover of *Dittrichia*. However, results from the multivariate analysis suggest that *Dittrichia* is capable of competing with other vegetation.

This study has important implications for directing resources for management and prevention of *Dittrichia* invasion. Off-road habitats are more at risk of invasion than many may have recognized, and such invasions could occur regardless of disturbance levels or species richness. This information is useful, especially for targeting invasive plant species in their introductory phase, before populations have expanded and become integrated into the community. Extending this research will provide further insight into biotic and abiotic factors that influence invasion of natural areas, which is crucial for protecting habitats with high conservation value from *Dittrichia* invasion across California and beyond. This study may also be applicable to other invasive plant species with similar patterns of spread along transport corridors.

I plan to expand this study beyond Santa Clara County and extend the data collected to include such environmental factors and resources as moisture, nutrients, light, and microbes. A bigger sample size would help clarify non-significant trends in the data. Better understanding of factors influencing *Dittrichia* invasion away from roadsides allows us to focus on the most vulnerable locations and make well informed decisions on where resources should be allocated for management. This insight is crucial for protecting vulnerable species and habitats from invasion.

Acknowledgements

I would like to thank Ingrid Parker, Nicky Lustenhouwer, and Miranda Melen for their support, feedback, and assistance throughout this project. They have provided me with an invaluable experience, many opportunities, and the tools required to achieve growth and success. I would also like to express my gratitude towards the CAMINO program at UCSC for allowing me to pursue my research by providing me with funding and continuous support.

References

Baker HG (1965) Characteristics and modes of origin of weeds. Charact Modes Orig Weeds 147–172.

Beaury EM, Finn JT, Corbin JD, Barr V, Bradley BA (2020) Biotic resistance to invasion is ubiquitous across ecosystems of the United States. Ecol Lett 23:476–482. https://doi.org/10.1111/ele.13446

Braasch J, Barker BS, Dlugosch KM (2019) Expansion history and environmental suitability shape effective population size in a plant invasion. Mol Ecol 28:2546–2558. https://doi.org/10.1111/mec.15104

Brownsey RN, Kyser GB, DiTomaso JM (2013a) Stinkwort is rapidly expanding its range in California. Calif Agric 67:110–115. https://doi.org/10.3733/ca.v067n02p110

Brownsey RN, Kyser GB, DiTomaso JM (2013b) Seed and germination biology of *Dittrichia graveolens* (stinkwort). Invasive Plant Sci Manag 6:371–380. https://doi.org/10.1614/IPSM-D-12-00072.1

Brownsey RN, Kyser GB, DiTomaso JM (2014) Growth and phenology of *Dittrichia graveolens*, a rapidly spreading invasive plant in California. Biol Invasions 16:43–52. https://doi.org/10.1007/s10530-013-0501-4

Byers JE, Noonburg EG (2003) Scale dependent effects of biotic resistance to biological invasion. Ecology 84:1428–1433. https://doi.org/10.1890/02-3131

Byers JE, Smith RS, Pringle JM, Clark GF, Gribben PE, Hewitt CL, Inglis GJ, Johnston EL, Ruiz GM, Stachowicz JJ, Bishop MJ (2015) Invasion expansion: time since introduction best predicts global ranges of marine invaders. Sci Rep 5:12436. https://doi.org/10.1038/srep12436

Christen D, Matlack G (2006) The role of roadsides in plant invasions: a demographic approach. Conserv Biol 20:385–391. https://doi.org/10.1111/j.1523-1739.2006.00315.x

Chytrý M, Jarošík V, Pyšek P, Hájek O, Knollová I, Tichý L, Danihelka J (2008) Separating habitat invasibility by alien plants from the actual level of invasion. Ecology 89:1541–1553. https://doi.org/10.1890/07-0682.1

Connell JH (1978) Diversity in tropical rain forests and coral reefs. Science 199:1302–1310. https://doi.org/10.1126/science.199.4335.1302

Frenkel RE (1977) Ruderal vegetation along some California roadsides. University of California Press.

Fridley JD, Stachowicz JJ, Naeem S, Sax DF, Seabloom EW, Smith MD, Stohlgren TJ, Tilman D, Holle BV (2007) The invasion paradox: reconciling pattern and process in species invasions. Ecology 88:3–17. https://doi.org/10.1890/0012-9658(2007)88[3:TIPRPA]2.0.CO;2

Gelbard JL, Belnap J (2003) Roads as conduits for exotic plant invasions in a semiarid landscape. Conserv Biol 17:420–432. https://doi.org/10.1046/j.1523-1739.2003.01408.x

Goldstein LJ, Suding KN (2014) Applying competition theory to invasion: resource impacts indicate invasion mechanisms in California shrublands. Biol Invasions 16:191–203. https://doi.org/10.1007/s10530-013-0513-0

Goslee SC, Urban DL (2007) The ecodist package for dissimilarity-based analysis of ecological data. J Stat Softw 22:1–19. https://doi.org/10.18637/jss.v022.i07

Grime JP (1974) Vegetation classification by reference to strategies. Nature 250:26–31. https://doi.org/10.1038/250026a0

Grime JP (1977) Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. Am Nat 111:1169–1194. https://doi-org.oca.ucsc.edu/10.1086/283244

Hansen MJ, Clevenger AP (2005) The influence of disturbance and habitat on the presence of non-native plant species along transport corridors. Biol Conserv 125:249–259. https://doi.org/10.1016/j.biocon.2005.03.024

Hughes R, Byrnes JE, Kimbro DL, Stachowicz JJ (2007) Reciprocal relationships and potential feedbacks between biodiversity and disturbance. Ecol Lett 10:849–864. https://doi.org/10.1111/j.1461-0248.2007.01075.x

Huston MA, Huston MA (1994) Biological diversity: the coexistence of species. Cambridge University Press.

Levine JM, Adler PB, Yelenik SG (2004) A meta-analysis of biotic resistance to exotic plant invasions: biotic resistance to plant invasion. Ecol Lett 7:975–989. https://doi.org/10.1111/j.1461-0248.2004.00657.x

Levine JM, Vilà M, Antonio CMD, Dukes JS, Grigulis K, Lavorel S (2003) Mechanisms underlying the impacts of exotic plant invasions. Proc R Soc Lond B Biol Sci 270:775–781. https://doi.org/10.1098/rspb.2003.2327

Luisa BG (2012) The ecology of natural disturbance and patch dynamics. Academic Press.

Mackey RL, Currie DJ (2016) The diversity-disturbance relationship: is it generally strong and peaked? Wiley.Collection. https://doi.org/10.6084/M9.FIGSHARE.C.3297515

Parendes LA, Jones JA (2000) Role of light availability and dispersal in exotic plant invasion along roads and streams in the H. J. Andrews Experimental Forest, Oregon. Conserv Biol 14:64–75. https://doi.org/10.1046/j.1523-1739.2000.99089.x

Preston RE (1997) *Dittrichia graveolens* (Asteraceae), new to the California weed flora. Madroño 44:200–203. https://www.jstor.org/stable/41426268

Radosevich SR, Stubbs MM, Ghersa CM (2003) Plant invasions: process and patterns. Weed Sci 51:254–259. https://doi.org/10.1614/0043-1745(2003)051[0254:PIPAP]2.0.CO;2

Rejmánek M (1996) Species richness and resistance to invasions. In: Orians GH, Dirzo R, Cushman JH (eds) Biodiversity and Ecosystem Processes in Tropical Forests. Springer Berlin Heidelberg, Berlin, Heidelberg, pp 153–172. https://doi-org/10.1007/978-3-642-79755-2_8

Schroeder J, Thomas SH, Murray LW (2005) Impacts of crop pests on weeds and weed–crop interactions. Weed Sci 53:918–922. https://doi.org/10.1614/WS-04-052R1.1

Shabani F, Ahmadi M, Kumar L, Solhjouy-fard S, Shafapour Tehrany M, Shabani F, Kalantar B, Esmaeili A (2020) Invasive weed species' threats to global biodiversity: future scenarios of changes in the number of invasive species in a changing climate. Ecol Indic 116:1-10. https://doi.org/10.1016/j.ecolind.2020.106436

Simberloff D (2010) Invasions of plant communities – more of the same, something very different, or both? Am Midl Nat 163:220–233. https://doi.org/10.1674/0003-0031-163.1.220

Simberloff D (2003) How Much Information on Population Biology Is Needed to Manage Introduced Species? Conserv Biol 17:83–92. https://doi.org/10.1046/j.1523-1739.2003.02028.x

Standish RJ, Cramer VA, Hobbs RJ (2008) Land-use legacy and the persistence of invasive *Avena barbata* on abandoned farmland. J Appl Ecol 45:1576–1583. https://doi.org/10.1111/j.1365-2664.2008.01558.x

Stohlgren TJ, Barnett DT, Kartesz JT (2003) The rich get richer: patterns of plant invasions in the United States. Front Ecol Environ 1:11–14. https://doi.org/10.1890/1540-9295(2003)001[0011:TRGRPO]2.0.CO;2

Stohlgren TJ, Binkley D, Chong GW, Kalkhan MA, Schell LD, Bull KA, Otsuki Y, Newman G, Bashkin M, Son Y (1999) Exotic plant species invade hot spots of native plant diversity. Ecol Monogr 69:25–46. https://doi.org/10.1890/0012-9615(1999)069[0025:EPSIHS]2.0.CO;2

Stohlgren TJ, Bull KA, Otsuki Y, Villa CA, Lee M (1998) Riparian zones as havens for exotic plant species in the central grasslands. Plant Ecol 138:113–125. https://doi.org/10.1023/A:1009764909413

Tyser RW, Worley CA (1992) Alien flora in grasslands adjacent to road and trail corridors in Glacier National Park, Montana (U.S.A.). Conserv Biol 6:253–262. https://doi.org/10.1046/j.1523-1739.1992.620253.x

Ward SF, Taylor BS, Dixon Hamil K-A, Riitters KH, Fei S (2020) Effects of terrestrial transport corridors and associated landscape context on invasion by forest plants. Biol Invasions 22:3051–3066. https://doi.org/10.1007/s10530-020-02308-3

Westbrooks RG (1998) Invasive plants: changing the landscape of America. All U.S. Government Documents (Utah Depository). Paper 490.

Westbrooks RG (2004) New approaches for early detection and rapid response to invasive plants in the United States. Weed Technol 18:1468–1471. https://doi.org/10.1614/0890-037X(2004)018[1468:NAFEDA]2.0.CO;2

Williamson M, Fitter A (1996) The varying success of invaders. Ecology 77:1661–1666. https://doi.org/10.2307/2265769

Yan J, Zhu Z, Huang H, Wang X, Sui H, Qiu D, Bai J, Cui B (2020) Stage-dependent effects of a non-native invasive saltmarsh plant on the seedling establishment of a native seagrass. Ecohydrol Hydrobiol 20:494–503. https://doi.org/10.1016/j.ecohyd.2019.08.002

Tables

Table 1. Latitude, longitude, and elevation data for each of the 30 total populations.

Population	Latitude	Longitude	Elevation (feet)
SCV Water District (Off-road)	37°14'46" N	121°52'22" W	190
SCV Water District (Roadside)	37°14'35" N	121°52'29" W	190
Baylands Park (Offroad)	37°24'50" N	121°59'43" W	10
Baylands Park (Roadside)	37°24'50" N	122°0'5" W	10
Lake Cunningham Park (Off-road)	37°20'17" N	121°48'43" W	120
Lake Cunningham Park (Roadside)	37°20'18" N	121°48'39" W	130
South San Jose VTA (Off-road)	37°14'13" N	121°47'15" W	210
South San Jose VTA (Roadside)	37°14'13" N	121°47'17" W	210
Coyote Creek Field (Off-road)	37°15'31" N	121°47'21" W	180
Coyote Creek Field (Roadside)	37°15'27" N	121°47'25" W	210
Alviso Bay Trail (Off-road)	37°25'14" N	122°1'3" W	10
Alviso Bay Trail (Roadside)	37°25'0" N	122°0'59" W	10
Calero Reservoir (Off-road)	37°11'9" N	121°46'28" W	470
Calero Reservoir (Roadside)	37°11'14" N	121°46'28" W	490
Campbell Percolation Ponds (Off-road)	37°15'57" N	121°57'16" W	240
Campbell Percolation Ponds (Roadside)	37°15'57" N	121°57'18" W	240
Lexington Reservoir (Off-road)	37°11'59" N	121°59'9" W	690
Lexington Reservoir (Roadside)	37°12'2" N	121°59'9" W	680
Metcalf Ponds (Off-road)	37°13'41" N	121°45'9" W	230
Metcalf Ponds (Roadside)	37°13'39" N	121°45'8" W	230
Penitencia Creek (Off-road)	37°23'38" N	121°50'18" W	260
Penitencia Creek (Roadside)	37°23'38" N	121°50'23" W	230
Parkway Lakes RV (Off-road)	37°10'43" N	121°41'24" W	310
Parkway Lakes RV (Roadside)	37°10'43" N	121°41'17" W	320
Chesboro Reservoir (Off-road)	37°7'32" N	121°42'25" W	540
Chesboro Reservoir (Roadside)	37°7'33" N	121°42'26" W	560
Oakridge Pond (Off-road)	37°15'17" N	121°52'5" W	190
Oakridge Pond (Roadside)	37°15'22" N	121°51'58" W	190
Guadalupe Reservoir (Off-road)	37°11'53" N	121°52'45" W	610
Guadalupe Reservoir (Roadside)	37°11'52" N	121°52'47" W	640

Figures

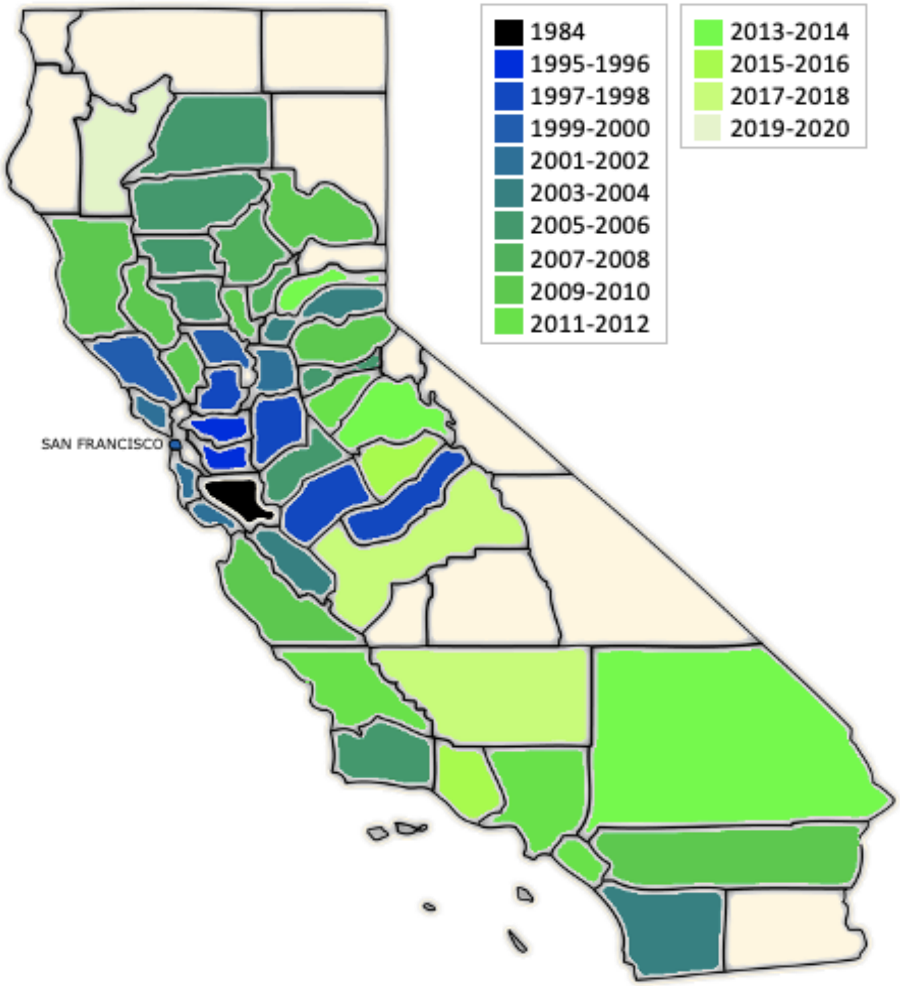

Figure 1. Map of California showing the range expansion of *Dittrichia graveolens* by county using point data. Adapted from Brownsey et al. (2013a) with additional data from California Agriculture and recent observations from Calflora.

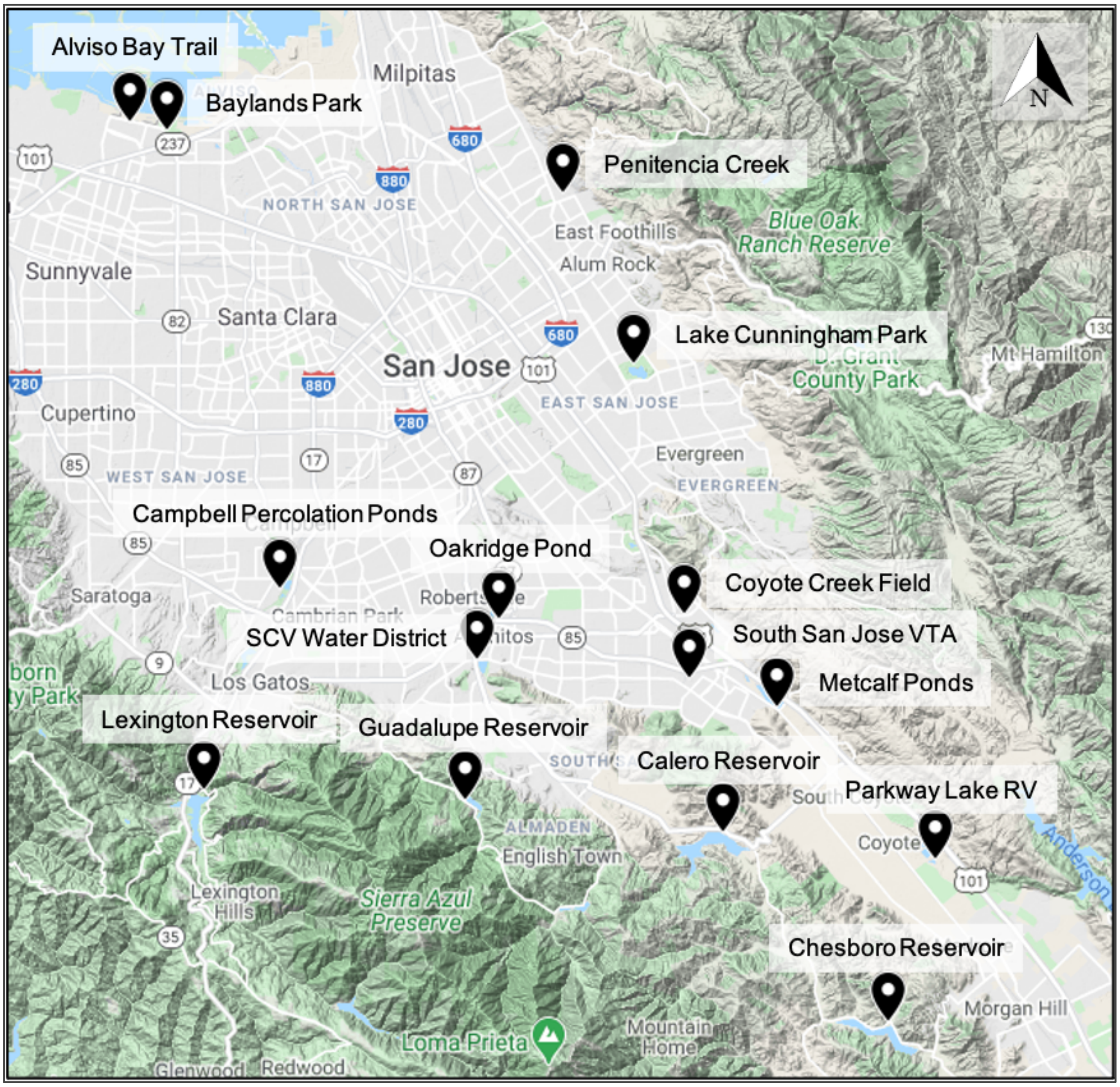

Figure 2. Map showing the 15 survey locations throughout Santa Clara County.

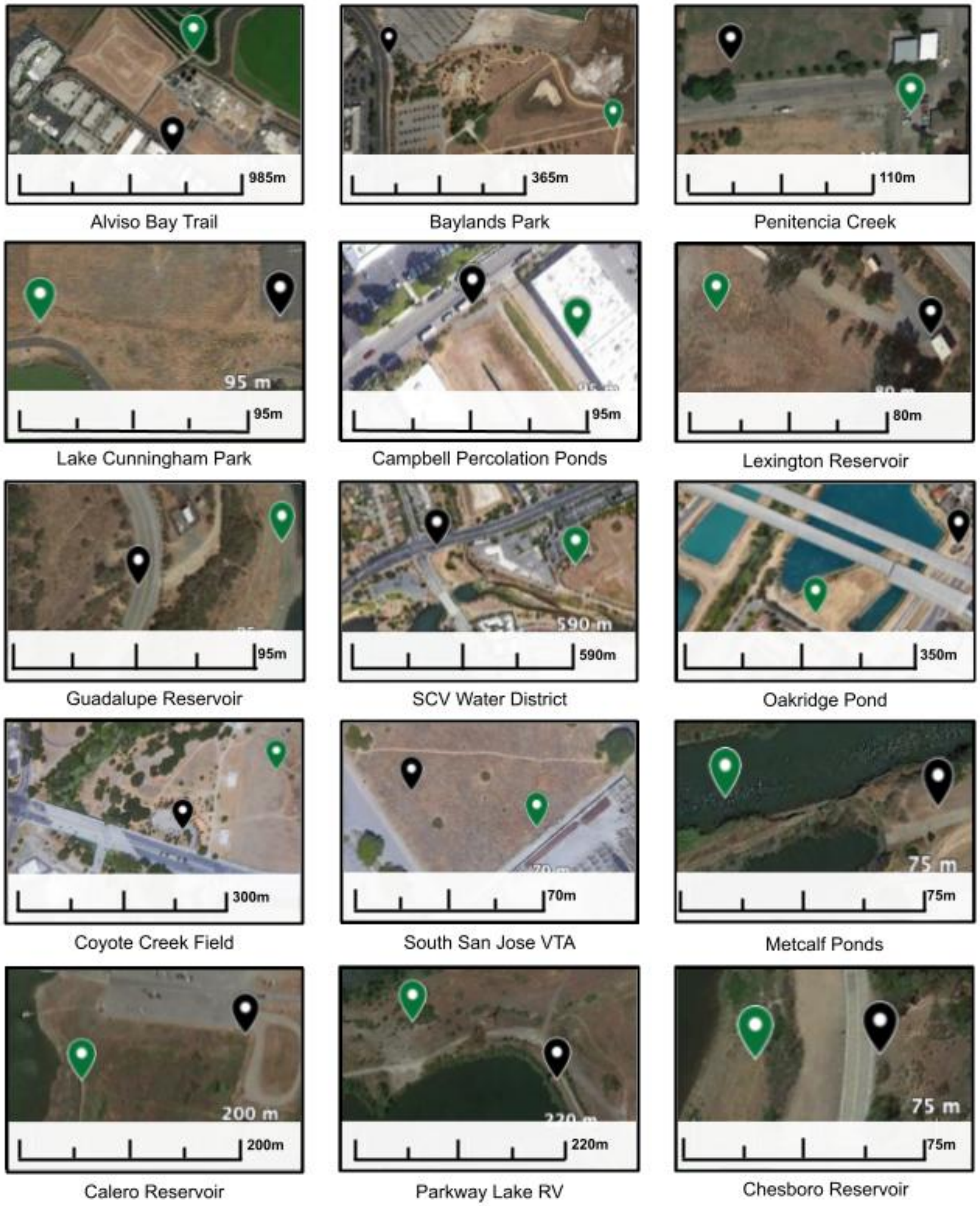

Figure 3. Map showing all 15 population pairs used in this study. Pairs include a roadside (black) population and a complimentary off-road (green) population.

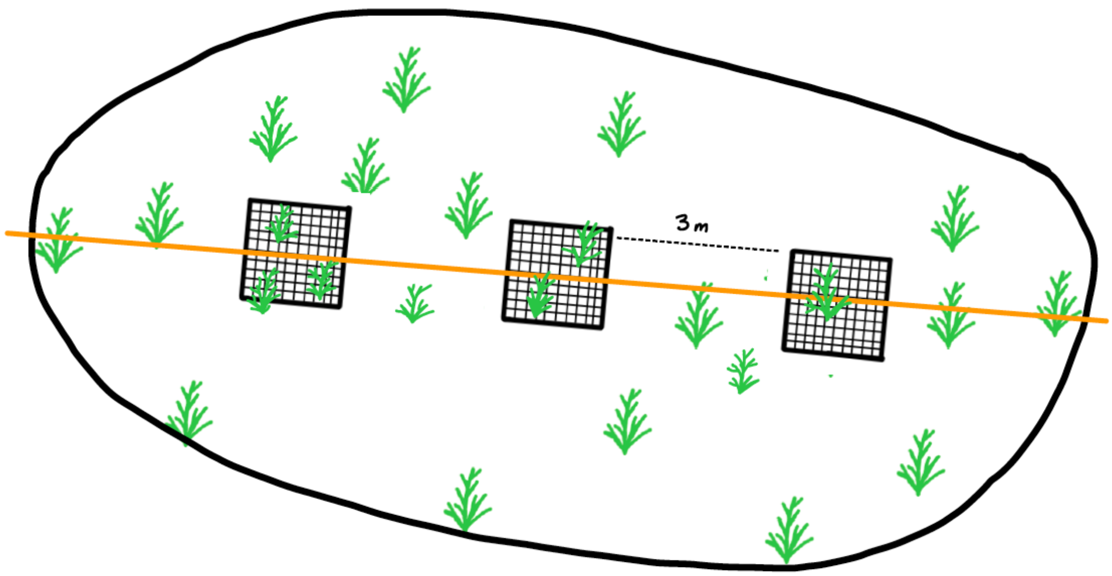

Figure 4. Example of survey design with transect (orange) laid across the longest axis of the population. The center quadrat was located at the midpoint of the transect and the other two quadrats were located 3 meters to the left and right of the midpoint.

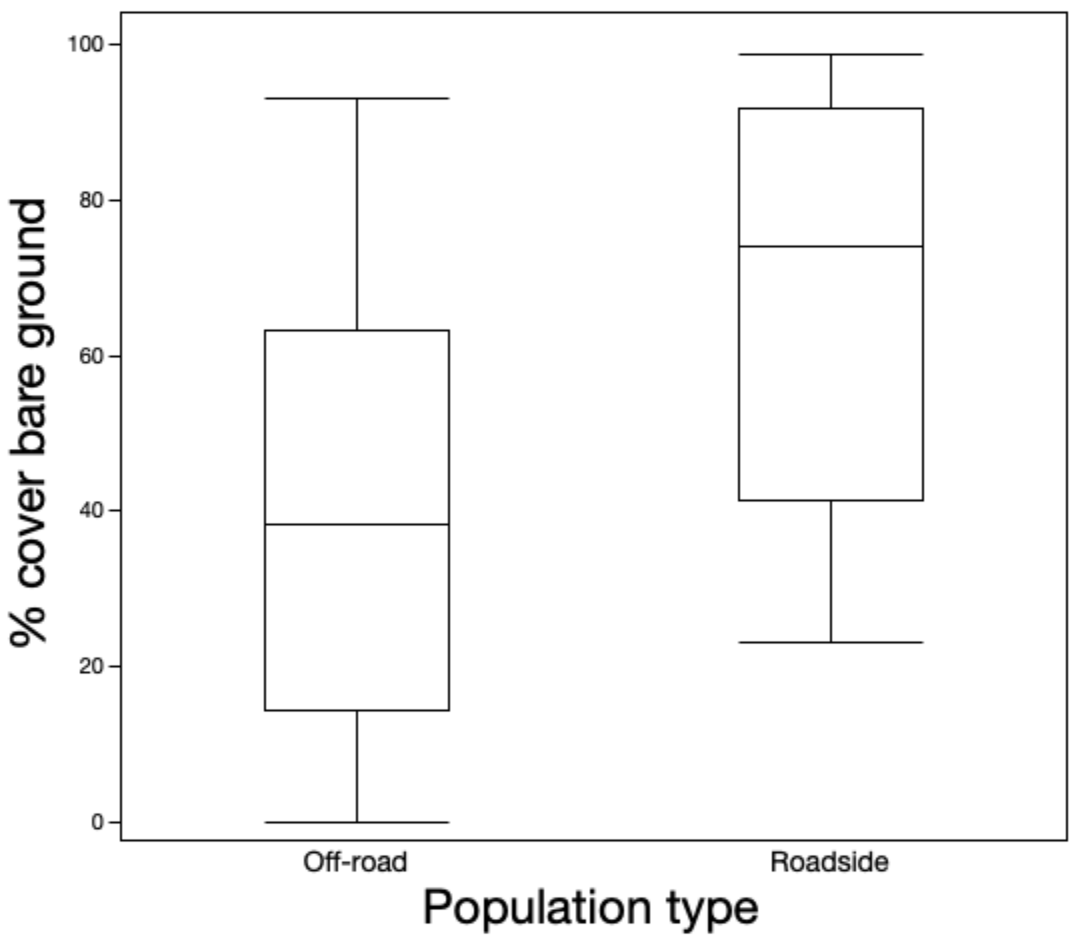

Figure 5. Average % cover bare ground compared between all 15 pairs of roadside and off-road sites.

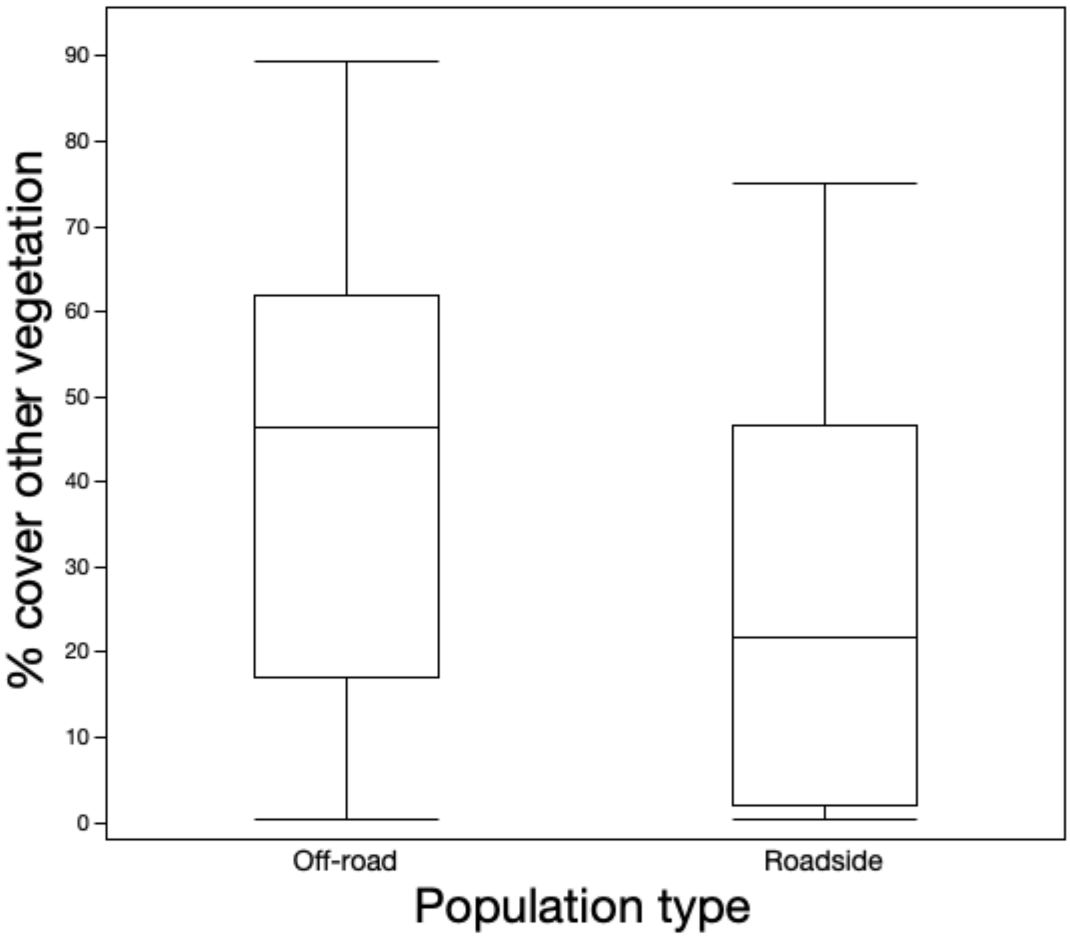

Figure 6. Average % cover of other (non-*Dittrichia*) vegetation compared between all 15 roadside and off-road sites.

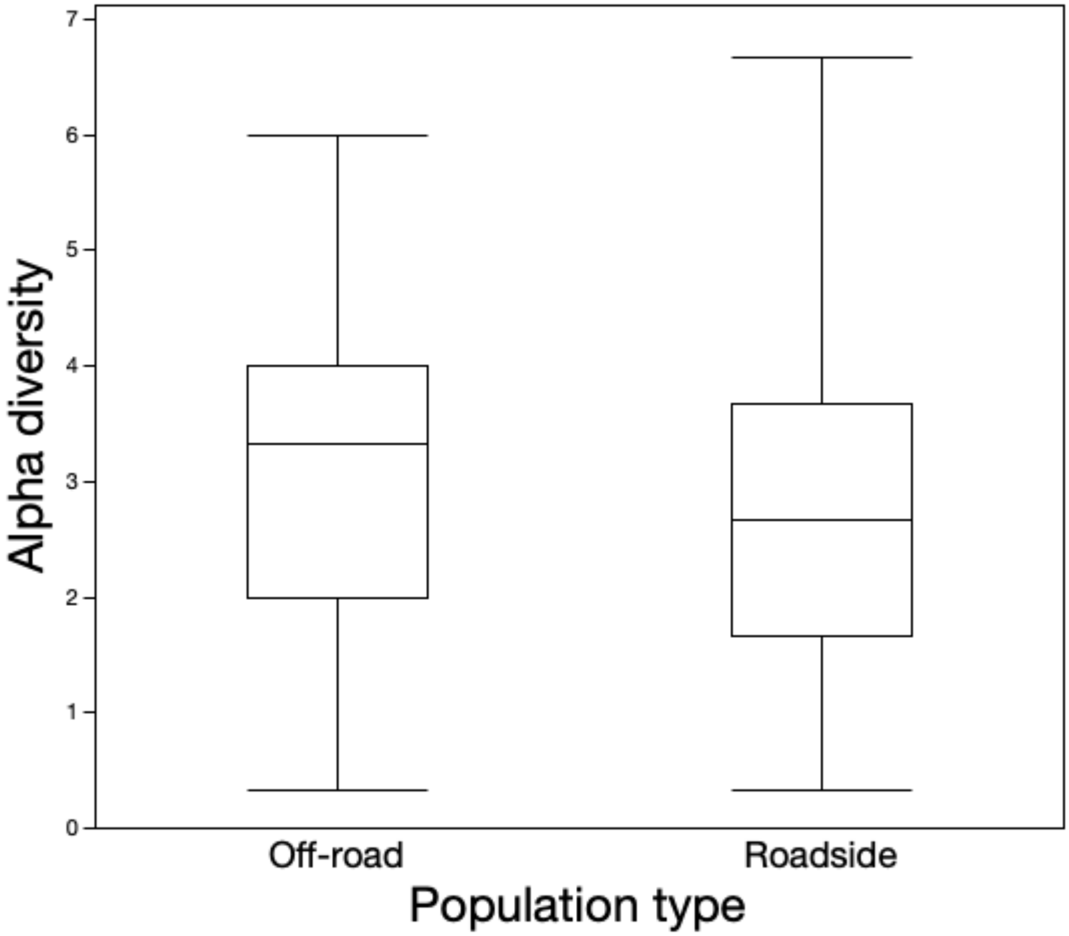

Figure 7. Quadrat level alpha diversity compared between roadside and off-road populations. Alpha diversity was averaged for three $0.25m^2$ quadrat samples from each population.

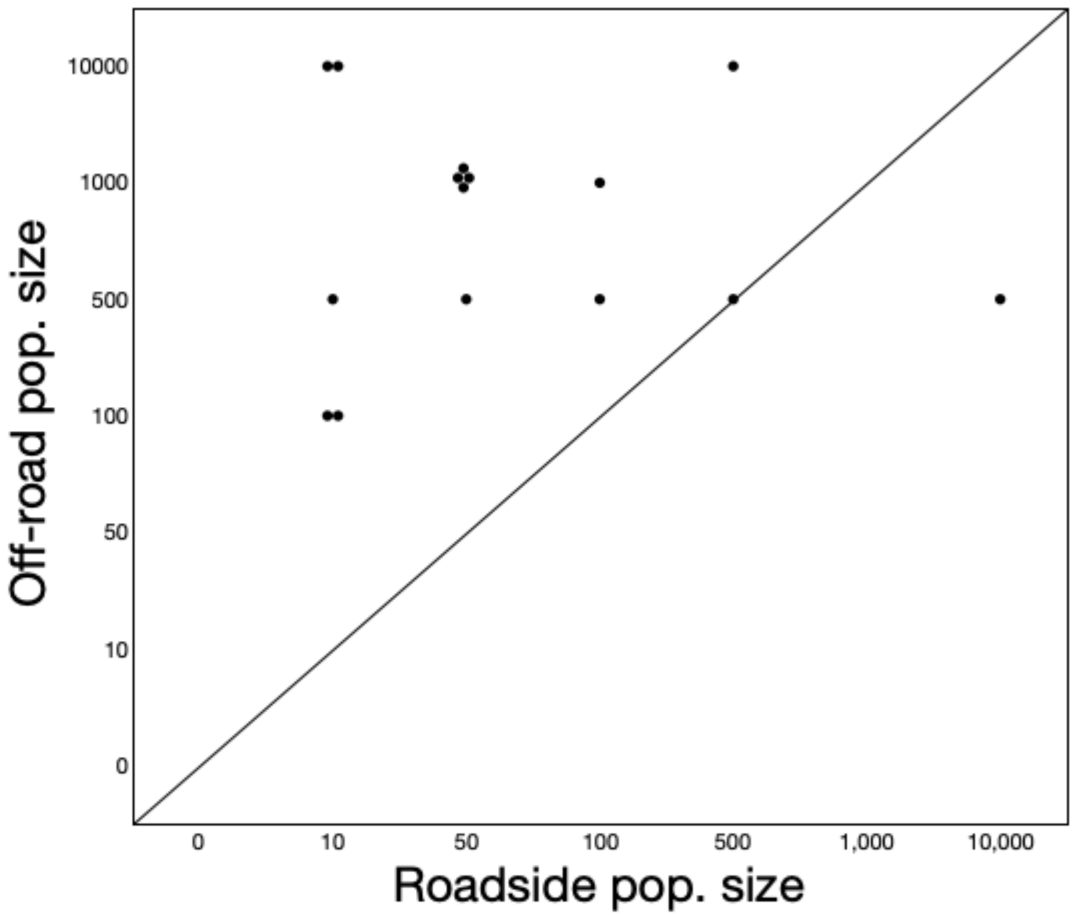

Figure 8. A comparison of population size between roadside and off-road pairs for all 15 locations. A one-to-one line was fit in JMP Pro 15 software. A non-significant trend towards larger populations off-road was observed.

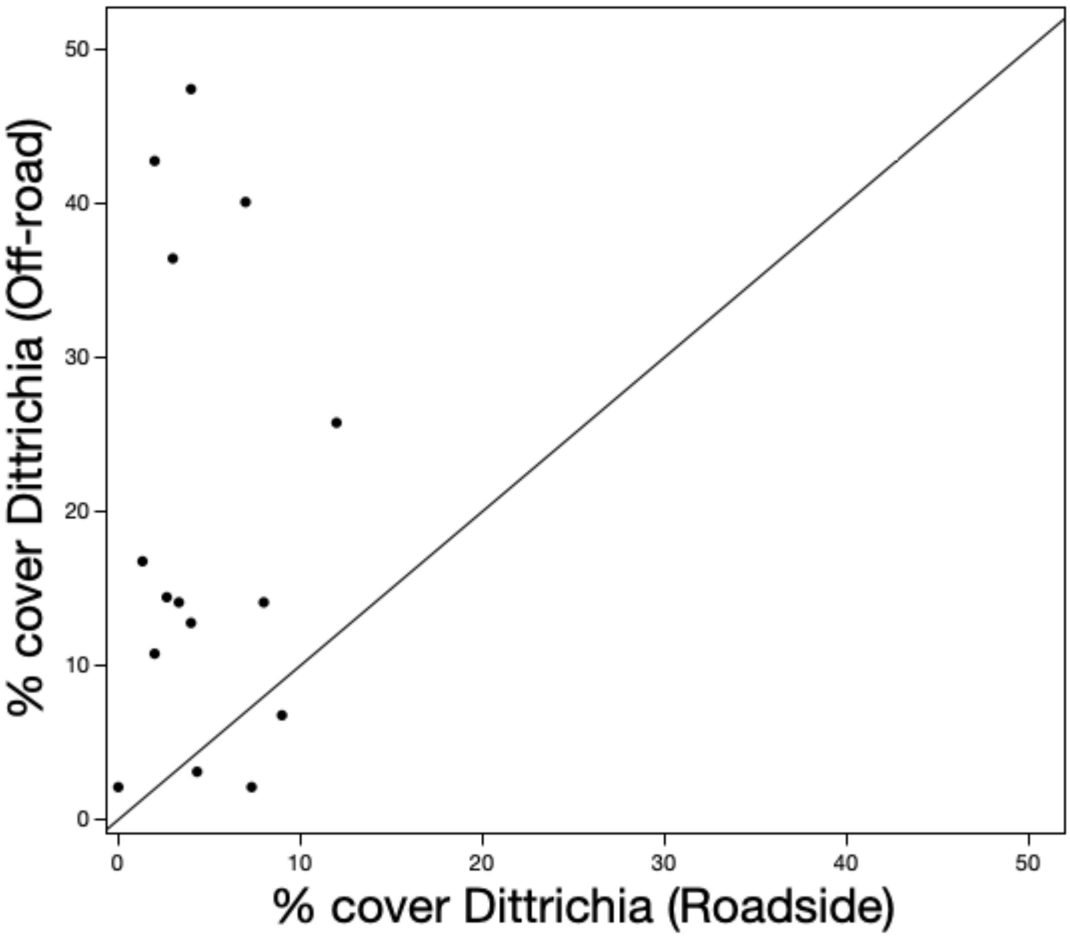

Figure 9. Comparison of average % cover *Dittrichia* for all 15 roadside and off-road pairs. A one-to-one line was fit using JMP Pro 15 software. Off-road sites had significantly higher percent cover *Dittrichia* compared to roadside sites.

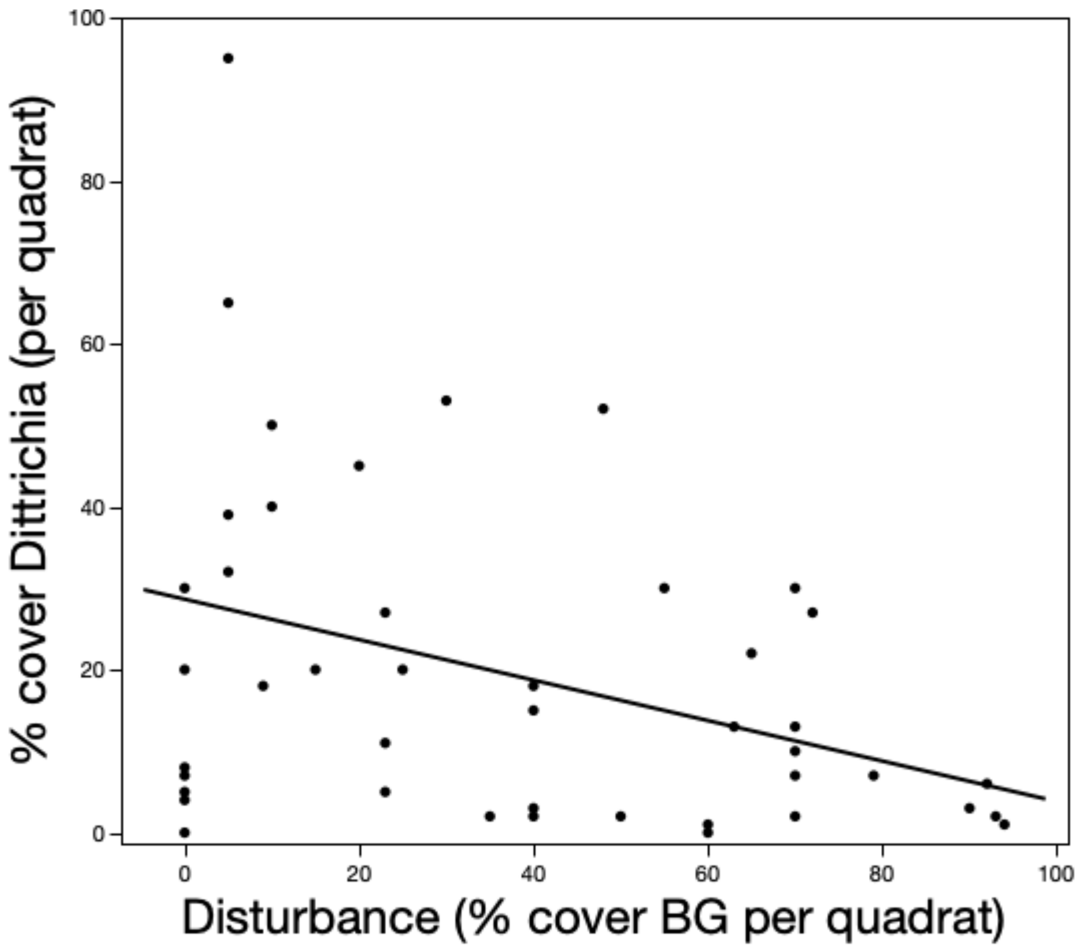

Figure 10. Regression between *Dittrichia* density inside quadrat and degree of disturbance (% cover bare ground) inside quadrat for all off-road populations. The line is least squares regression.

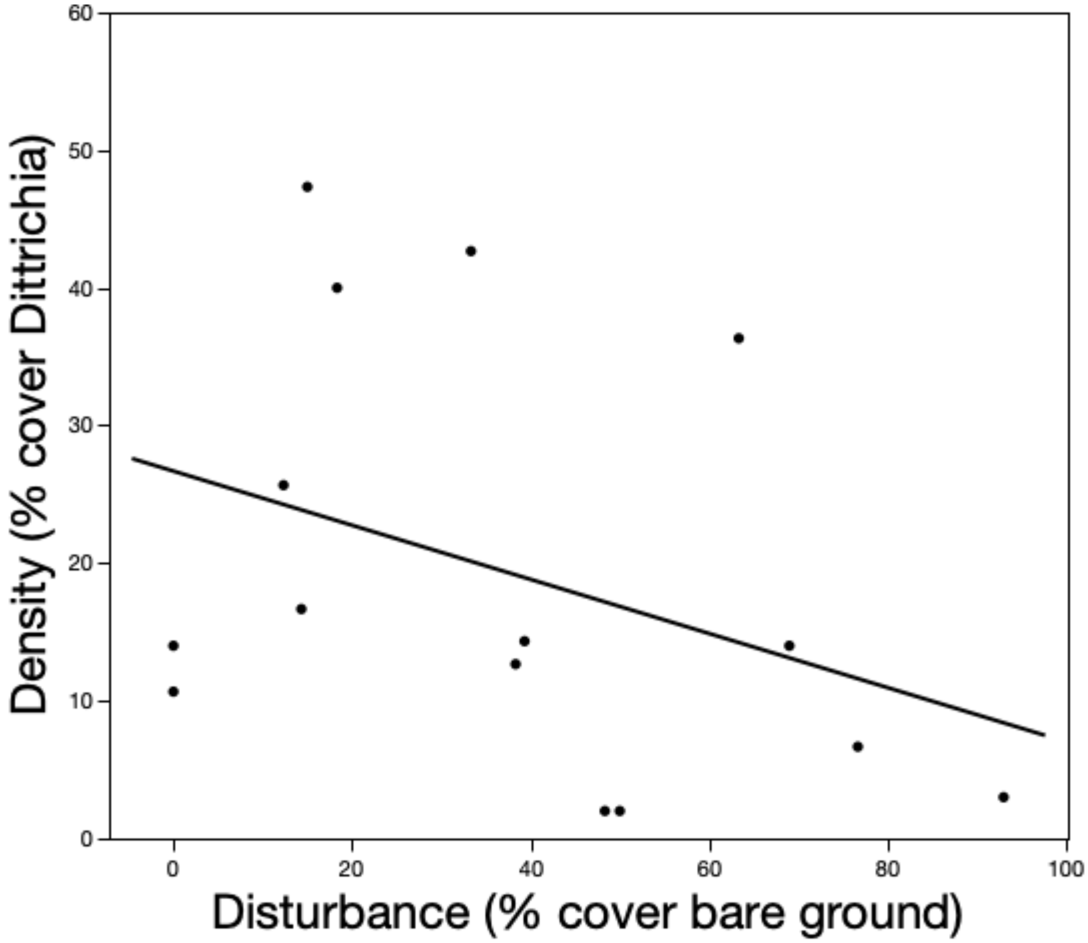

Figure 11. Regression between *Dittrichia* density (% cover *Dittrichia*) and disturbance (% cover bare ground) for off-road populations only. The line is least squares regression.

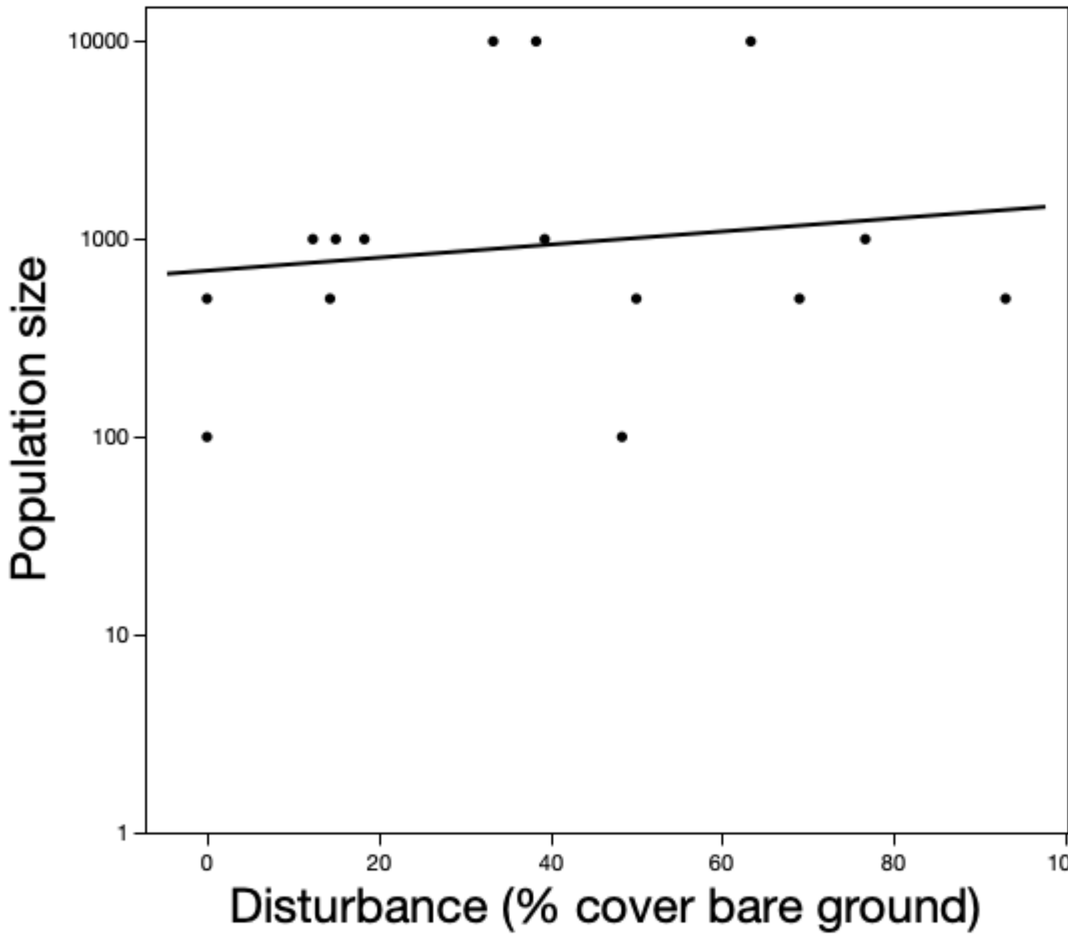

Figure 12. Regression between % cover bare ground and population size for off-road populations only. The line is least squares regression.

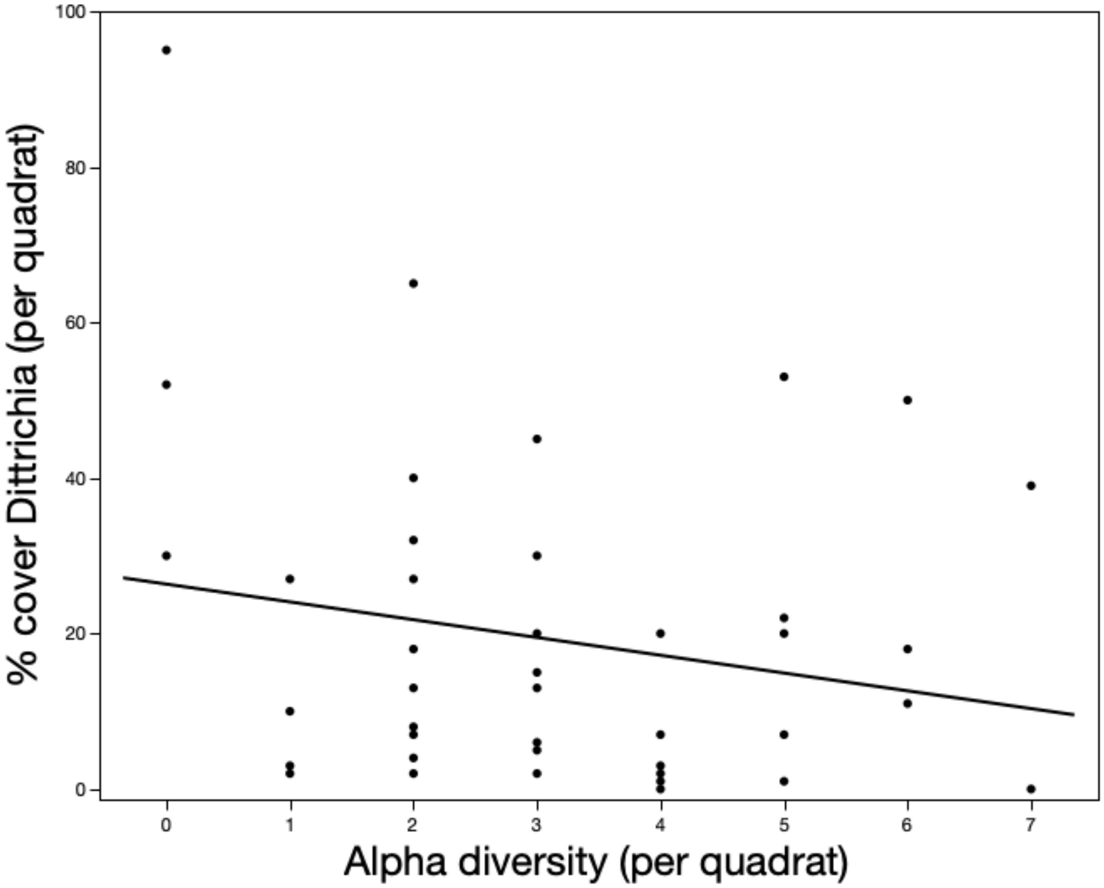

Figure 13. Regression of quadrat level *Dittrichia* cover by quadrat level alpha diversity for all off-road populations. Each population was sampled 3 times using a quadrat. The line is least squares regression.

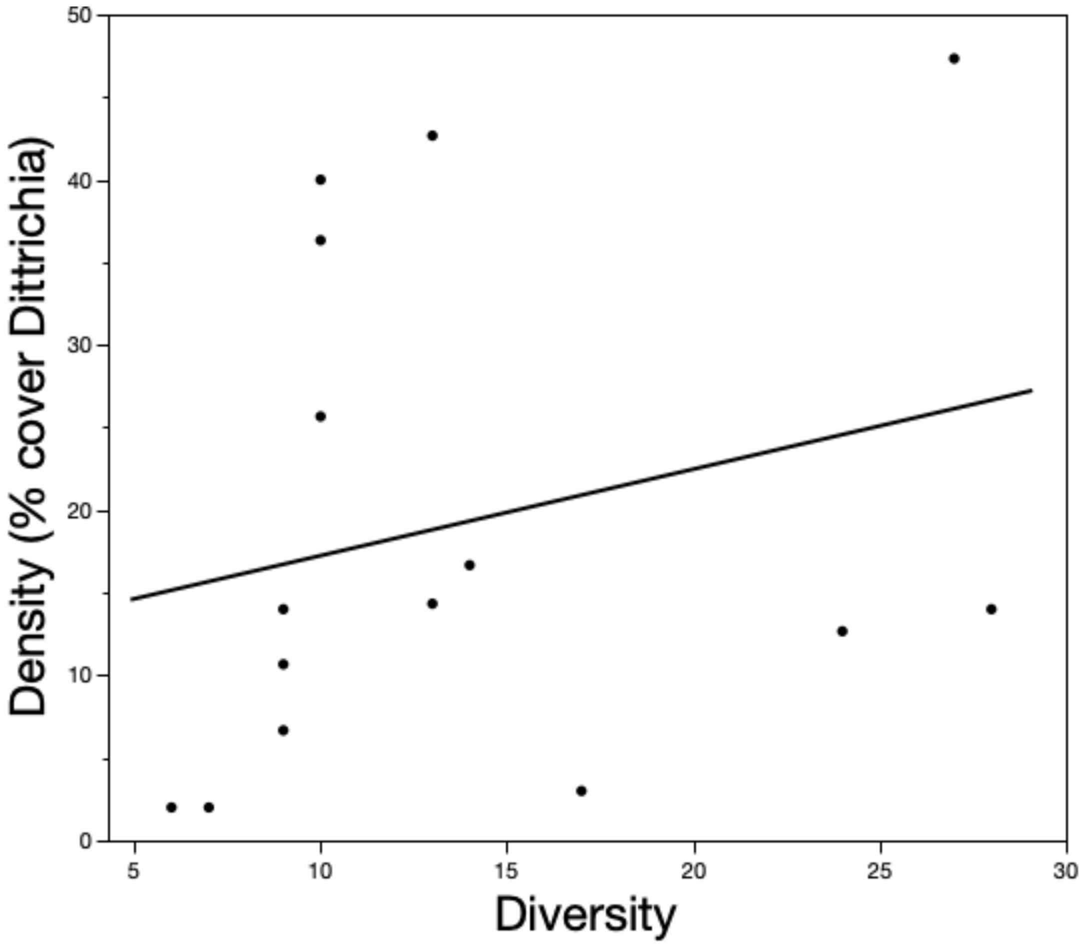

Figure 14. Regression between alpha diversity (# of species) and density (% cover *Dittrichia*) for 15 total off-road sites. The line is least squares regression.

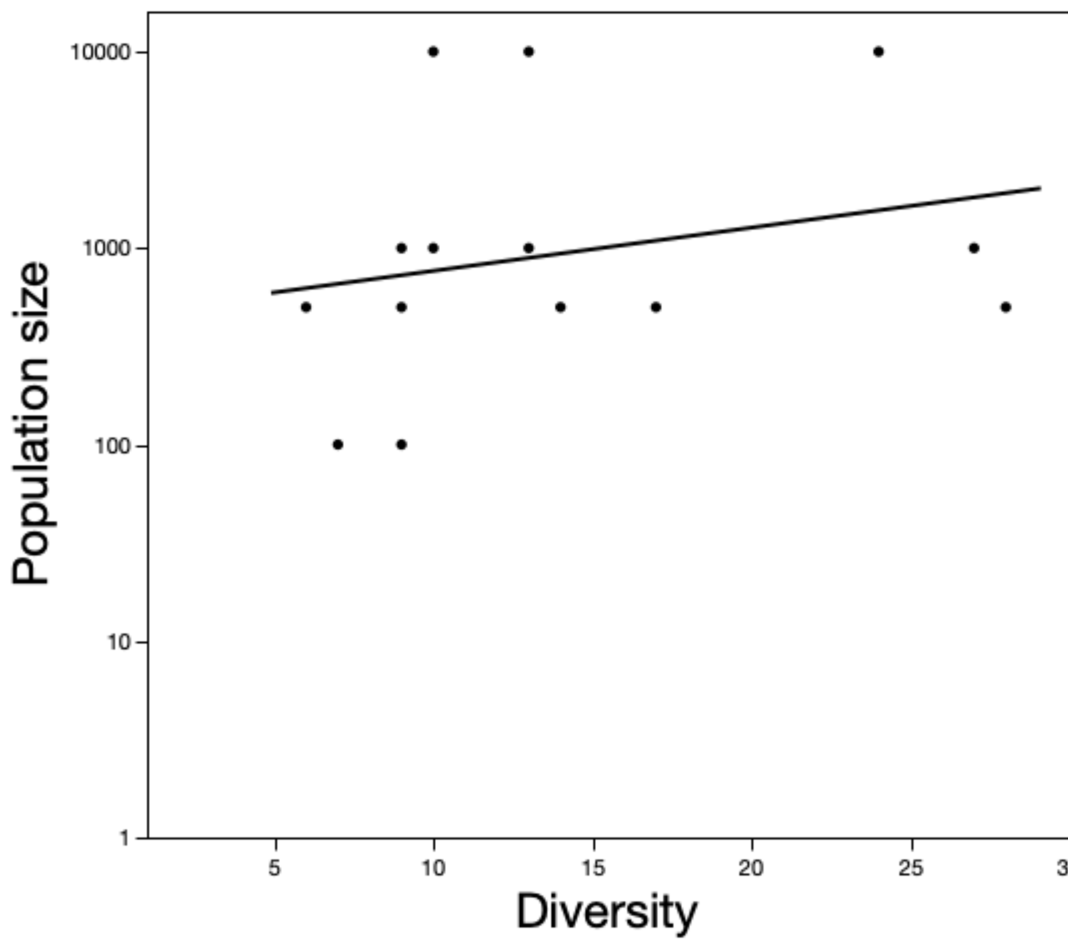

Figure 15. Regression of population size (# of individuals) and alpha diversity for all 15 off-road populations. The line is least squares regression.

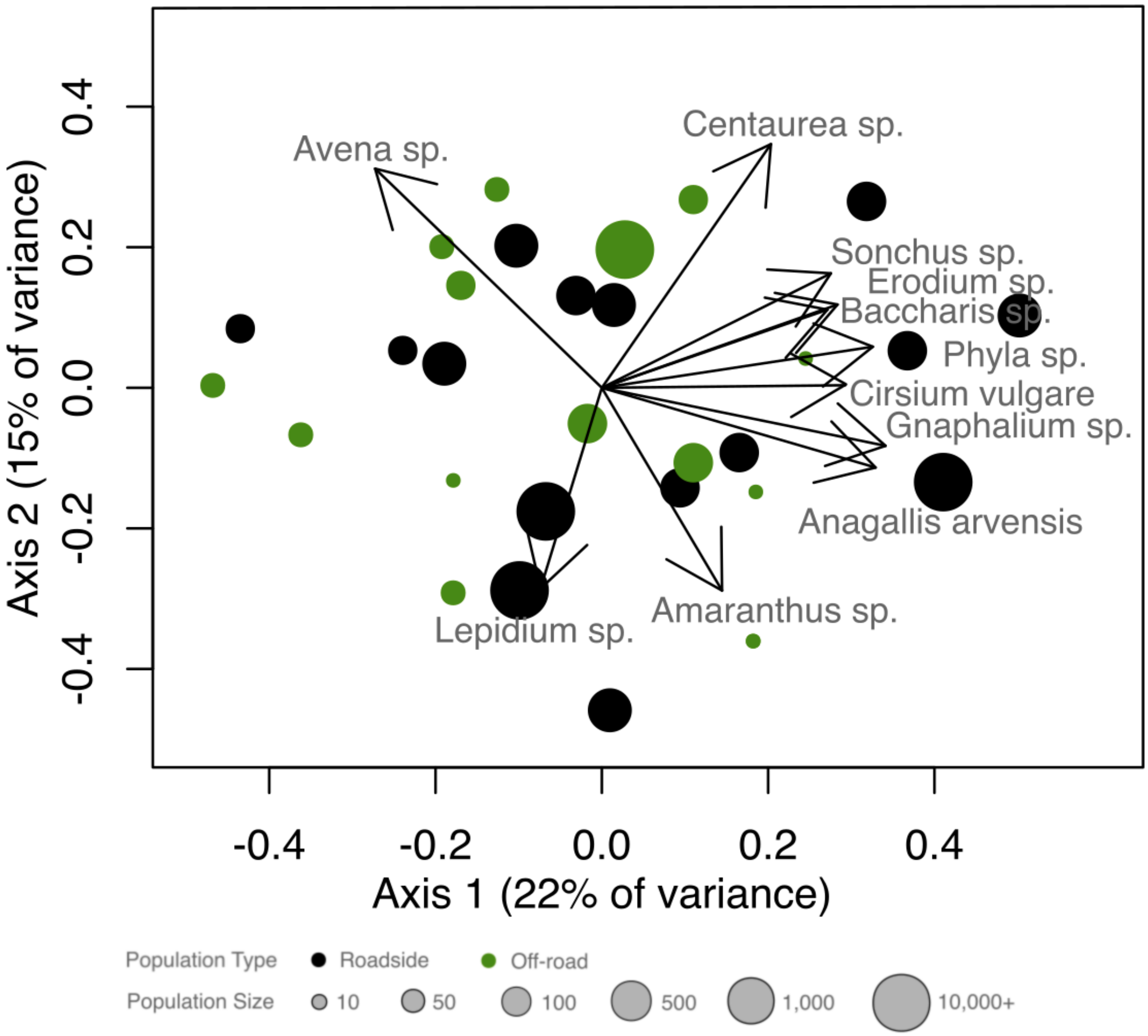

Figure 16. Circles are sites; black circles are roadside sites and green circles are off-road sites. The size of the circle represents the size of the *Dittrichia* population at that site. *Dittrichia* is not included in the original analysis of species composition.

Appendix A

Genus (Species if known)	Roadside Site Name														
	Alviso Bay Trail	Baylands Park	Calero Reservoir	Campbell Perc. Ponds	Chesboro Reservoir	Coyote Creek Field	Guadalupe Reservoir	Lake Cunningham	Lexington Reservoir	Metcalf Ponds	Oakridge Pond	Parkway Lakes RV	Penitencia Creek	SCV Water District	South San Jose VTA
Anagallis arvensis				X											
Aster #1 (unknown)														X	
Aster #2 (unknown)														X	
Avena sp.			X		X	X				X					
Baccharis pilularis									X						
Brassica nigra			X			X			X	X		X	X		
Bromus sp.	X		X	X	X	X	X			X	X	X	X	X	
Carduus pycnocephalus			X												
Centaurea solstitialis												X			
Cyclospermum sp.													X		
Epilobium sp.			X	X										X	X
Erigeron bonariensis		X		X									X		
Erigeron canadensis		X													
Erodium sp.	X				X									X	
Euphorbia sp.									X						
Foeniculum vulgare												X			
Genista sp.									X						
Gnaphalium palustre	X	X							X						
Grass sp. #3		X													
Helminthotheca sp.			X												
Lepidium sp.								X							
Lythrum sp.								X							
Malva sp.				X									X		
Medicago sp.				X	X								X		
Paspalum sp.	X														
Plantago sp.			X						X			X			
Polycarpon sp.				X									X		
Polygonum sp.								X						X	
Sonchus sp.	X		X	X			X						X		
Spergularia sp.					X										
Trifolium sp.					X										

	Off-road Site Name														
Genus (Species if known)	Alviso Bay Trail	Baylands Park	Calero Reservoir	Campbell Perc. Ponds	Chesboro Reservoir	Coyote Creek Field	Guadalupe Reservoir	Lake Cunningham	Lexington Reservoir	Metcalf Ponds	Oakridge Pond	Parkway Lakes RV	Penitencia Creek	SCV Water District	South San Jose VTA
Acmispon sp.															X
Anagallis arvensis					X							X			
Artemisia sp.									X						
Aster (unknown)														X	
Avena sp.		X	X									X			X
Baccharis pilularis					X		X		X			X	X		
Brassica nigra		X			X	X			X	X				X	
Bromus sp.	X		X	X		X		X		X	X				X
Carduus pycnocephalus	X														
Centaurea solstitialis										X		X			
Conium sp.										X					
Cynodon sp.							X								
Descurainia sp.									X						
Epilobium sp.	X				X		X			X		X		X	X
Erodium sp.					X						X				
Genista sp.									X						
Gnaphalium palustre					X		X		X					X	
Grass sp. #1		X													
Grass sp. #2		X													
Heliotropium sp.					X			X							
Helminthotheca sp.										X					
Heterotheca sp.												X			
Lactuca serriola				X											
Lepidium sp.	X							X							
Malva sp.				X											
Medicago sp.				X		X	X				X	X			
Melilotus sp.							X		X					X	
Mentha sp.										X					
Phyla sp.					X										
Polygonum sp.				X			X		X						
Polypogon monspeliensis			X		X		X		X					X	
Sonchus sp.												X			
Verbena sp.									X						