A cline within an ecotype of the yellow monkeyflower, *Mimulus guttatus*

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ABSTRACT

Premise: A key goal of evolutionary biologists is to understand how and why adaptive genetic variation is partitioned within species. In the yellow monkeyflower, *Mimulus guttatus* (syn. *Erythranthe guttata*), coastal perennial populations collectively constitute a single genetically and morphologically differentiated ecotype. While the distinctiveness of the coastal ecotype has now been well documented, there is also variation in environmental factors across the range of the coastal ecotype that could drive differentiation among its component populations in a more continuous way.

Methods: Based on previous observations of a potential cline within this ecotype, we quantified plant height across coastal perennial accessions from 69 total populations in two greenhouse common garden experiments. To evaluate possible environmental factors driving the relationship between plant height and latitude, we regressed height against multiple climatic factors, including temperature, precipitation, and coastal wind speeds.

Results: In both experiments, plant height was negatively correlated with latitude. *Mimulus* height correlated positively with annual precipitation and with mean wind speed, to a lesser degree, and negatively with annual mean temperature. We hypothesize that one or more of these factors drove clinal variation within the coastal ecotype.

Conclusion: Overall, our study illustrates the complexity of how the distribution of environmental variation can both simultaneously drive the evolution of distinct ecotypes as well as continuous clines within those ecotypes. These results are discussed in the context of the classic criticisms of ecotypes being intermediates in the process of speciation.

KEY WORDS: Local adaptation, salt spray, *Erythranthe guttata*, wind, speciation

INTRODUCTION

A century ago, Turesson (1922a,b) recognized that adaptive phenotypic variation was often highly divergent in correlated sets of traits when comparing groups of populations derived from different habitats. Turesson referred to these groups of phenotypically similar, locally-adapted populations as ecotypes (Turesson 1922a,b; Gregor et al. 1936). Several researchers following Turesson found the concept of ecotypes useful for describing the distribution of adaptive genetic variation within species (Gregor et al. 1936; Clausen et al. 1948; Clausen 1951; Böcher 1967; Heywood 2011). Further, these researchers viewed ecotypes as an intermediate stage in the process of speciation and a way to directly link natural selection to the formation of new species (reviewed in Lowry 2012). However, other researchers doubted the validity of Turesson's ecotype concept and argued that clines (Huxley 1938) best represented how adaptive genetic variation is partitioned across the geographic distribution of a species' range (Langlet 1963; 1971; Stebbins 1980).

While some recent authors have concluded that the cline versus ecotype controversy has been resolved because adaptive genetic variation can be partitioned different ways depending on the distribution of selective factors across the range of a species (Linhart and Grant 1996; Briggs and Walters 2016), multiple questions still remain. Foremost among these questions is whether ecotypes do indeed represent intermediate stages in the formation of new species. Both Quinn (1978) and Levin (1993) argued that there was no way that ecotypes could be intermediate stages in the process of speciation because, in their view, formation of geographically widespread ecotypes would require uniform habitats to also be widespread across large geographic regions. This led Levin to conclude that most speciation in plants occurs in localized, isolated populations

(Levin 1993). However, if it can be shown that ecotypes can evolve despite a lack of uniformity of habitat conditions, it would support the hypothesis that widespread ecotypes are indeed a stage in the process of the formation of new species.

In this study, we examined whether there is a clinal distribution of phenotypic variation within a widespread ecotype of the yellow monkeyflower, *Mimulus guttatus* (syn. *Erythrante guttata*; Barker et al. 2012). *M. guttatus* exhibits high levels of genetic and phenotypic variation across its extensive range across western North America, which makes it a particularly useful system for studying local adaptation (Vickery 1978; Lowry et al. 2008). Coastal perennial populations of *M. guttatus*, occurring from southern California to southern Washington State, collectively comprise a distinct ecotype based on population genetic data (Lowry et al. 2008; Twyford and Friedman 2015). This ecotype has been designated as a variety (*M. guttatus var. grandis* Greene) or species (*M. grandis* syn. *E. grandis*; Barker et al. 2012, Nesom 2012, 2014) by taxonomists. Despite these taxonomic designations, due to its morphological distinctiveness, the coastal perennial ecotype is highly interfertile with other populations of *M. guttatus* (Lowry and Willis 2010). Further, there were only four fixed genetic differences between the coastal perennial and inland annual populations out of 29,693,578 SNPs surveyed in a population genetic study of this system (Gould et al. 2017). Based on these results, we believe that it is best to think of the coastal perennial populations as intraspecific genetic variation within the *Mimulus guttatus* species complex (Lowry and Willis 2010; Twyford and Friedman 2015; Gould et al. 2017).

Several previous studies of local adaptation in *M. guttatus* have found striking genetically-based phenotypic differences between the coastal perennial ecotype and nearby inland populations in the western United States (Vickery 1952; Hall et al. 2006, 2010; Lowry et al. 2008; Oneal et al. 2014). Many of the inland populations of *M. guttatus* have an annual life-history, especially those that occur in inland habitats that completely dry out during summer months (Vickery 1952; Clausen and Heisey 1958; Wu et al. 2008; Lowry et al. 2008). In contrast, the coastal perennial ecotype occurs in coastal habitats that are regularly damp and foggy during summer months (Vickery 1952; Clausen and Heisey 1958; Hitchcock and Cronquist 1973; Hall and Willis 2006; Lowry et al. 2008). In greenhouse common garden experiments, accessions derived from coastal habitats had thicker stems, many more prostrate stoloniferous branches, later flowering times, and produced far more herbivore defensive compounds than nearby inland annual populations (Hall et al. 2006, 2010; Lowry et al. 2008; Lowry and Willis 2010; Oneal et al. 2014; Lowry et al. 2019).

While there is both phenotypic and genetic divergence between ecotypes of *M. guttatus*, it is unclear to what extent genetic variation is present within individual ecotypes – either due to adaptation to widespread environmental gradients or idiosyncratic with regard to geographic space. However, a previous pilot study suggested the possibility that there may be a cline in plant height within the coastal ecotype (Lowry 2010). Since that initial study, dozens of additional coastal *M. guttatus* populations have been collected, which provides an opportunity for a more comprehensive survey of variation over the entire geographic range of the coastal perennial ecotype.

110 In this study, we tested the hypothesis that clinal phenotypic variation can occur within ecotypes
111 of a species. Specifically, we investigated several populations of coastal perennial *M. guttatus*
112 from across the ecotype's range to determine whether there was indeed a latitudinal cline in plant
113 height. To establish potential sources of selection, we examined whether there is a relationship
114 between the phenotypes of the accessions and the climates from where they were collected in
115 nature. Through these efforts, we attempted to understand whether clinal trait variation occurred
116 within a distinct ecotype, which would support the hypothesis that the evolution of
117 geographically widespread ecotypes does not require a widespread distribution of uniform
118 habitats, as argued by Quinn (1978) and Levin (1993).

119

120 **METHODS**

121 ***Germplasm for experiments –***

122 The seeds used in these experiments originated from natural population collections made
123 between 2004 and 2016. Seeds were either collected directly from plants in the field or collected
124 from plants that had been brought from the field back to the greenhouses at Duke University
125 (Durham, North Carolina, USA) or Michigan State University (East Lansing, Michigan, USA).
126 For each population, we collected location description information, habitat description, and GPS
127 coordinates. Photos of the plants in the field for each population have been posted on iNaturalist
128 and vouchers for a subset of the populations were deposited at the California Academy of
129 Sciences. Permits were obtained for collections on public lands, where permission was required.
130 All maternal families used in this study are currently stored at Michigan State University in
131 airtight containers with silica gel as a desiccant.

Greenhouse Experiments –

To determine whether there was clinal variation in *M. guttatus* height, we conducted two independent experiments in two different controlled greenhouse environments.

For the first experiment, seeds collected from coastal perennial *M. guttatus* were planted according to maternal family (*N* = 135 seed families, 56 populations) in 3.5 sq. in. pots with SUREMIX (Michigan Grower Products, Inc., Galesburg, Michigan, USA). We randomized these pots into flats (17 pots per flat) and stratified the seeds in a dark cold room (set to 4º C) for a week to encourage more uniform germination before being transferred to the greenhouses at Michigan State University. All germinating seedlings were removed from each pot, except for the centermost plant. Plants were bottom-watered approximately every other day throughout the remainder of the experiment. Plants were grown in the greenhouses with 16 h of supplemental lighting and room temperature set to 22º C. We measured plant height in centimeters for each plant at the time of first flower. Approximate germination dates and flowering dates were also recorded.

Based on promising results from the first experiment, we conducted a second greenhouse experiment to determine if the initial results would be replicable with a larger sample size (more populations and individuals) and in a different greenhouse. Seeds from coastal perennial *M. guttatus* (*N* = 402 seed families, 66 populations) were planted (SUREMIX, 3.5 sq. in. pots) without prior cold stratification, directly in Plant Ecology Field Lab greenhouse at Kellogg Biological Station (KBS, Hickory Corners, MI, USA). Each pot contained seeds from a single

maternal family and were randomized into flats in the same way as the first experiment. Again, pots were thinned to one plant and remaining individuals were watered every other day throughout the experiment. Germination and flowering dates were recorded, and plant height was measured (in cm) at the time of first flowering.

Climate Data –

To investigate potential environmental drivers of adaptive phenotypic variation, we extracted climatic data for each population's collection location of origin from the WorldClim Bioclimatic variables database (Fick and Hijmans 2017). This data was imported and compiled using R (v.3.6.0, R Core Team 2019).

In addition to the Bioclim data, we extracted oceanic wind speed data from along the US Pacific Coast using the National Renewable Energy Laboratory's Wind Prospector website, which featured interactive online maps of wind speeds surveyed by NREL (King et al. 2014; Draxl et al. 2015a,b). We used Pacific Monthly Offshore Wind Speed map layers to collect wind speeds for each month from the site nearest to shore (8 km offshore at the closest; Draxl et al. 2015b) at the latitudes of each of the coastal perennial populations. The wind speeds found through the NREL Wind Prospector were the averages for each 1.2 km X 1.2 km offshore site and were modeled at 100 m (Draxl et al. 2017). Due to unavailability of data outside of the contiguous US, populations found in British Columbia and Alaska (denoted by population codes ALA and LBG) were not included in climate data analyses. Monthly wind speed averages accessible via NREL were based on observations and statistical analyses over the course of seven years (King et al. 2014; Draxl et al. 2015a,b), which we used to calculate quarterly and annual wind speeds for

each population collection location. We then matched these climate variables with their corresponding coordinates and population codes for further analysis.

Statistical Analysis –

To test whether there was a relationship between plant height and the latitude of origin (location from which each population accession was collected), we conducted linear regression modeling using the R software package (v.3.6.0, R Core Team 2019). We conducted independent analyses for each of the two greenhouse experiments.

Although we predicted that latitude would correlate with plant height across space, we wanted to evaluate which climatic variables correlated with latitude might ultimately be driving observed clinal patterns. Climate variables are often highly correlated with each other, so we conducted a principal components analysis (PCA) to reduce the dimensionality of the data prior to further analyses. Climate data, described above, was extracted for each population and we performed the PCA in R. For both sets of greenhouse data, we utilized all principal components (PCs) with an eigenvalue greater than 1, following the Kaiser criterion (Kaiser 1960). We then conducted regression analyses of plant height against each of these PCs, again using linear models in R. All data organization, analysis, and visualization were conducted in R Studio.

RESULTS

Plant height was negatively correlated with latitude –

Overall, we found a significant relationship between population latitude and plant height in both Greenhouse Experiment 1 (Multiple $R^2 = 0.24$, $F_{1,54} = 16.71$, $P < 0.001$, $N = 56$ populations; 135

individuals) and Greenhouse Experiment 2 ($R^2 = 0.37$, $F_{1,64} = 36.83$, $P < 0.001$, $N = 66$ populations; 402 individuals). In both experiments, coastal perennial *M. guttatus* height was negatively correlated with latitude (Figures 1, 2). Based on our linear modeling, we found that every degree latitude further north translated to roughly 1 cm decrease in plant height under greenhouse conditions (Experiment 1 slope = -0.95; Experiment 2 slope = -1.12).

The relationship of climatic factors and plant height for Experiment 1 –

To gain further insight into the possible causes of the negative relationship between latitude and plant height, we conducted principal component analyses of climate factors. For Greenhouse Experiment 1, we focused our analyses on climate PC1 through PC4, as all of them had eigenvalues greater than 1. These 4 PCs accounted for 94.55% of cumulative variance in the climate factors; PC1 explained 59.03% of the variation, followed by PC2 at 19.57%, PC3 at 11.13%, and PC4 at 4.82%. We found that PC1 had a significant negative relationship with plant height (*Multiple* $R^2 = 0.22$, $F_{1,54} = 14.97$, $P < 0.001$, slope = -0.72). The other three PCs were not significantly correlated with plant height ($P > 0.05$).

Given that PC1 had a significant negative correlation with height, we investigated which climate variables were most highly loaded on this PC axis. The most heavily loaded variables on PC1 were Annual Precipitation, Average Annual Temperature, Precipitation of the Wettest Quarter, and Precipitation of the Coldest Quarter. Annual Temperature was negatively correlated with PC1, while all others were positively correlated. While not as heavily loaded, Average Wind Speeds in Quarter 1 and Quarter 4 were both positively correlated with PC1. Additional variables that were significantly loaded on PC1 included Precipitation of the Wettest Month, Precipitation

Seasonality, Precipitation of the Warmest Quarter, and Average Temperature of the Coldest Quarter. More specific information regarding loadings and coordinates of individual climate variables on PC1 can be found in Table 1.

The relationship of climatic factors and plant height for Experiment 2 –

For Greenhouse Experiment 2, we found that PC1 through PC6 all had eigenvalues greater than 1. In total, those 6 PCs accounted for 98.33% of cumulative variance in climate factors. PC1 explained the most variation at 55.93%, followed by PC2 with 22.94%, PC3 with 10.88%, PC4 with 3.87%, PC5 with 2.65%, and PC6 with 2.07%. PC1 was significantly negatively correlated with plant height (*Multiple* $R^2 = 0.39$, $F_{1,62} = 39.53$, $P < 0.001$, slope = -1.25). As in Experiment 1, none of the other 5 PCs were significantly correlated with plant height ($P > 0.05$).

As we did for Experiment 1, we evaluated which climatic factors loaded onto PC1. Heavily loaded climate variables included Annual Precipitation and Average Annual Temperature, in addition to Precipitation Seasonality, Precipitation of the Warmest Quarter, and Precipitation of the Wettest Quarter. Of these variables, Average Annual Temperature and Precipitation Seasonality were negatively correlated with PC1, while the others were positively correlated (Table 2). The Average Wind Speed in Quarters 1 and 4 were also loaded on PC1, but not as strongly as the other factors.

Latitude strongly predicts climate for coastal populations –

While latitude can be a weak predictor of climate, especially for continental populations, we suspected that it might be highly correlated with climate in our study, as all populations were distributed latitudinally along a coastline. To assess how well latitude predicts climate for these

populations, we regressed the extracted principal components from both greenhouse experiments against latitude. These analyses confirmed that many of the climate variables involved were highly correlated with latitude. Using the principal components from Experiment 1, we found that PC1 had a very strong positive relationship with latitude (*Multiple* $R^2 = 0.93$, $F_{1,54} = 689$, $P < 0.001$, slope = 0.76). The other PCs were not significantly correlated with latitude ($P > 0.05$). Just as for Experiment 1, PC1 of Experiment 2 was the only PC significantly associated with latitude (*Multiple* $R^2 = 0.91$, $F_{1,62} = 652.1$, $P < 0.001$, slope = 0.85). To determine how well variation in individual climatic factors was predicted by latitude, we regressed all the climate factors that were highly loaded on PC1 individually against latitude. Those results are reported in Table 1.

Patterns of wind speed along the west coast of North America –

Plants are well known to respond to wind through changes in growth form (Grace 1977; Gardiner et al. 2016; Telewski 2021). This, combined with the observation of wind speed loading onto the first PC of climate, led us to evaluate the patterns of wind speed variation more carefully across the populations that we studied. We found that, in general, annual wind speeds increase with latitude (*Multiple* $R^2 = 0.06$, $F_{1,76} = 4.465$, $P = 0.038$, slope = 0.07). Average wind speeds in Quarter 1 (*Multiple* $R^2 = 0.46$, $F_{1,76} = 65.9$, $P < 0.001$, slope = 0.19) and Quarter 4 (*Multiple* $R^2 = 0.50$, $F_{1,76} = 75.32$, $P < 0.001$, slope = 0.27) of the year follow this pattern closely, although Quarter 2 wind speeds (*Multiple* $R^2 = 0.20$, $F_{1,76} = 19.1$, $P < 0.001$, slope = -0.20) showed a negative relationship with latitude. Quarter 3 wind speeds were not correlated with latitude (*Multiple* $R^2 = 0.01$, $F_{1,76} = 0.57$, $P > 0.05$, slope = 0.05). A key realization from this analysis is that patterns of wind speed variation shift dramatically across seasons and have a

striking non-linear relationship with latitude. This nonlinear relationship can be observed in visualizations of annual and quarterly average wind speeds: after initially increasing with latitude, average wind speeds generally decrease with latitude for populations north of southern Oregon (42º N) (Figure 3). Across seasons, wind speeds slow down during the summer much more in the southern end of the range of the coastal populations, while remaining high in northern California and southern Oregon throughout the summer months.

DISCUSSION

In this study, we found a significant negative relationship between latitude and genetically-based differences in plant height within the coastal ecotype of *M. guttatus*. This clinal pattern was likely driven by adaptation to climate variables that are correlated with latitude along the coast of the Pacific Ocean. Populations of *M. guttatus* collected from the southern end of the range were repeatedly found to be taller in common garden experiments than more northern populations. These southern populations generally experience higher temperatures, less precipitation, and lower velocity winds than more northern populations, especially during summer months. The results of this study further reinforce the idea that adaptive genetic variation can be simultaneously partitioned in disjunct (among ecotypes) and continuous (clinal) ways. Overall, our results have implications for the evolution of adaptive genetic variation in this system, as well as general implications for the longstanding criticism of the hypothesis that ecotypes are intermediates in the evolution of plant species.

The finding of clines within ecotypes helps shape our understanding of the evolution of new plant species –

Understanding the patterns by which genetic variation is partitioned among populations within a species across a geographic landscape has been a matter of considerable debate, especially in the classic plant evolutionary biological literature (reviewed in Lowry 2012). It is reasonable to hypothesize that the partitioning of that genetic variation is a function of how environmental variation is partitioned across the same landscape. However, several previous researchers have argued against the existence of ecotypes and that only clinal variation exists within species (Langlet 1971; Quinn 1978; Stebbins 1980; Levin 1993).

A series of prior studies has clearly established that the coastal populations of *Mimulus guttatus* from central California to southern Washington state collectively comprise a genetically distinct geographically widespread ecotype (Lowry et al. 2008; Lowry and Willis 2010; Oneal et al. 2014; Twyford and Friedman 2015). This coastal perennial ecotype clusters as a distinct group from the rest of the *Mimulus guttatus* species complex based on both a set of morphological traits and allele frequencies of loci across the genome (Lowry 2012; Oneal et al. 2014; Twyford andFriedman 2015) but has not accumulated appreciable divergence through fixed genetic differences (Gould et al. 2017).

While genomic data has allowed us to address the classic criticism about the existence of geographically widespread ecotypes made by Langlet (1971) and others, it is the discovery of clines within ecotypes that allows us to address doubts about how those ecotypes could come

307 into existence in the first place. Both Quinn (1978) and Levin (1993) expressed doubt about the
308 evolution of geographically widespread ecotypes evolving within species because they
309 hypothesized that uniform habitats would also necessarily be widespread to facilitate the
310 concerted evolution of new widespread ecotypes. Levin (1993) took this argument a step further
311 and argued that most speciation in plants must be local and thus, follow a model of peripatric
312 speciation. Levin's argument was built off those of Raven (1980), who concluded that there was
313 no logical way that geographically widespread ecotypes or subspecies could eventually evolve
314 into distinct species.

315

316 The level of environmental change across the range of the coastal ecotype of *M. guttatus*
317 demonstrates that habitats with uniform environments are not necessary for the evolution of
318 geographically widespread ecotypes. Further, the finding of a cline within the coastal ecotype
319 suggests that that nonuniformity of climate across the range of an ecotype can drive adaptative
320 phenotypic variation within an ecotype, while other shared climate factors simultaneously
321 maintain the divergence of that ecotype from the rest of a species complex. Indeed, this should
322 not be a surprising conclusion, as clines within coastal ecotypes/species have been observed in
323 the classic literature for plant systems such as *Plantago maritima* (Gregor 1930, 1938) and
324 *Achillea borealis* (Clausen et al. 1948).

325

326 Overall, the conclusion that widespread ecotypes exist as intermediates in the evolution of new
327 species fits the emerging modern paradigm of speciation based on recent results from genomic
328 studies. In those studies, there is increasing evidence that introgression (i.e., gene flow) occurs at

329 various stages during the process of species splitting into distinct phylogenetic lineages
330 (Reviewed in Mallet et al. 2015; Taylor and Larson 2019; Edelman and Mallet 2021). This
331 model of speciation with gene flow is not the same as classic models of sympatric speciation,
332 which require consistent gene flow throughout the entire process of speciation (Coyne andOrr
333 2004). Instead, recent genomic studies suggest that it takes considerable time, with successive
334 bouts of sympatry and allopatry for distinct, fully reproductively isolated phylogenetic lineages
335 to become established (Mallet et al. 2015; Taylor and Lason 2019; Edelman and Malet 2021).
336 Further, a recent review by Levin (2012) supports the long period over which the speciation
337 process is completed in plants. During the long period over which new lineages evolve,
338 ecotypes/subspecies will evolve clines and locally adapted populations within their boundaries.
339 Many of these ecotypes/subspecies will go extinct or merge fully back into broader species
340 complexes. Others will eventually become fully reproductively isolated lineages, but only after
341 multiple bouts of gene flow with other members of the species complex. In the case of the
342 coastal perennial ecotype of *M. guttatus*, the population genetic evidence suggests that it was
343 derived at a single point in time from the rest of the species complex and then spread along the
344 Pacific coast, adapting to local environments as it spread (Lowry et al. 2008; Twyford &
345 Frianddman 2015). During and following the spread of the coastal ecotype, there has likely been
346 appreciable gene flow with other parts of the species complex, which is further supported by
347 there only being four fixed nucleotide differences between these groups out of millions of SNPs
348 (Gould et al. 2017).

349

350 ***The environmental factors responsible for the cline in plant height –***

While we have demonstrated that a cline in plant height does occur within the coastal ecotype of *Mimulus guttatus*, the question remains as to what environmental factors have driven this cline. Though our analysis identified multiple factors correlated with both latitude and plant height, these factors must be carefully considered, as they are autocorrelated with each other and not all of them may have impact on the selective advantage of plant height.

Other researchers studying the evolution of ecotypes in the same region have found similar patterns in plant height variation along the Pacific coast of North America. These studies were far less comprehensive, but are useful, as they suggest that the patterns observed within the coastal ecotype of *M. guttatus* are not unique. For example, Clausen et al. (1948) found similar genetic variation with the coastal ecotype of *Achillea borealis*, when comparing populations in Northern California, where populations north of the San Francisco Bay were shorter in stature than those from farther south in California in common garden experiments.

While temperature and precipitation were most highly correlated with latitude and thus, plant height in our study, it is difficult to conceptualize a mechanistic hypothesis of how those factors would drive the evolution of the cline in plant height. In contrast, the spatial-temporal distribution of winds speeds along the Pacific coast, while less closely correlated with latitude, due to its non-linear distribution, is more likely to have driven the cline in plant height. Onshore wind from the ocean can be intense along the Pacific Coast, depending on the location and time of year (Grace 1977; Gilliam 2002). The intensity of wind speed increases with the distance above the ground (Grace 1977; Jaffe and Forbes 1993). While wind can be damaging by itself, it

is particularly damaging to plants along ocean coastlines because it contains aerosolized oceanic salt spray (Boyce 1954; Barbour 1978; Cheplick and Demetri 1999; Griffiths et al. 2006; Kouali et al. 2017; Du and Hesp 2020). Unlike stress caused by soil salinity, salt spray primarily damages plants by landing directly on aboveground tissues and entering through stomata and small cracks in the cuticle (Grieve andPitman 1978; Du and Hesp 2020). Boyce (1954) recognized that this compact growth form is advantageous for coastal plants because it helps them to avoid the impacts of salt spray by being more sheltered from the wind. Prior research has demonstrated that the coastal perennial ecotype of *M. guttatus* is consistently more tolerant to salt spray in laboratory assays than the inland annual ecotype (Lowry et al. 2009). However, these assays could not assess how the combination of wind speeds and salt spray could drive the evolution of plant architecture.

We hypothesize that the evolution of the cline in height of the coastal perennial ecotype is a function of the interaction of time and space of wind speeds along the Pacific coast. Across the range of the ecotype, wind speeds and wave energy that drive salt spray are greater in the spring (April, May) than the summer (July, August) (Gilliam 2002; Garcia-Reyes and Largier 2012). However, those winds speeds dissipate most during the summer in the region south of the San Francisco, especially in more protected areas, like the Monterey Bay (Figure 2b), where plants in the field reach up to two meters in height (Lowry *personal observation*). In Northern California and Southern Oregon, high coastal windspeeds remain elevated throughout the summer months, which coincides with when this species flowers. Since reproductive structures are often the most sensitive to salt spray (Griffiths et al. 2006), maintaining a compact growth form when flowering under higher windspeed/salt spray conditions is likely to be advantageous. While this hypothesis

works well to explain the results for populations from central California to southern Oregon, it does not hold up for central and Northern Oregon, where windspeeds are generally reduced during summer months. This suggests that other environmental factors are responsible for maintaining a compact stature in this region or that these populations are shorter in stature due to evolutionary history. Evolutionary history could be responsible for the short stature of the northernmost populations, if they are descended from populations from windier regions to the south. Alternatively, the northern region of Oregon could have had higher wind speeds in the recent past, which drove their present-day short stature. Future population genomic studies could establish whether the observed geographic patterns could be a result of evolutionary history. Further, tests to establish whether reduced height is an adaptation to wind and salt spray could be conducted by growing populations of various heights in a common garden experiment at a windy coastal location.

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AUTHOR CONTRIBUTIONS

DBL conceived of and oversaw the experiments and analyses. TZ conducted the experiments and analyses. Both authors wrote the manuscript.

DATA AVAILABILITY STATEMENT

All data will be made available at publication, either as supplementary information or on Dryad.

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578 **TABLES**

Table 1. Regressions of climate factors that were highly-loaded on PC1 for both experiments against latitude

Greenhouse Experiment 1		Estimate	F	Multiple R^2	P
	Annual Precipitation	0.045939	401.9	0.8816	< 2.2e-16
	Mean Annual Temperature	-2.3367	237.2	0.8146	< 2.2e-16
	Wettest Quarter Precipitation	0.09784	239.6	0.8161	< 2.2e-16
	Coldest Quarter Precipitation	0.10375	200.9	0.7882	< 2.2e-16
	Mean Wind Speed, 1st Quarter	2.1737	50.06	0.4811	3.11E-09
	Mean Wind Speed, 4th Quarter	1.6486	74.6	0.5801	9.37E-12
	Wettest Month Precipitation	0.2877	191.4	0.7799	< 2.2e-16
	Precipitation Seasonality	-0.27944	607.2	0.9183	< 2.2e-16
	Warmest Quarter Precipitation	0.58611	470.4	0.897	< 2.2e-16
	Mean Temperature, Coldest Quarter	-1.8891	163.2	0.7514	< 2.2e-16
Greenhouse Experiment 2					
	Annual Precipitation	0.048022	242.2	0.7962	< 2.2e-16
	Mean Annual Temperature	-2.538	315.9	0.8359	< 2.2e-16
	Precipitation Seasonality	0.29744	553.1	0.8992	< 2.2e-16
	Warmest Quarter Precipitation	0.60288	430.6	0.8741	< 2.2e-16
	Wettest Quarter Precipitation	0.10225	169.2	0.7318	< 2.2e-16
	Mean Wind Speed, 1st Quarter	2.3456	47.42	0.4334	3.38E-09
	Mean Wind Speed, 4th Quarter	1.8108	67.49	0.5212	1.68E-11
	Coldest Quarter Precipitation	0.108175	143.3	0.698	< 2.2e-16
	Driest Quarter Precipitation	0.5965	372.9	0.8574	< 2.2e-16
	Driest Month Precipitation	2.5381	223.7	0.783	< 2.2e-16
	Wettest Month Precipitation	0.30039	143.6	0.6984	< 2.2e-16
	Mean Temperature, Coldest Quarter	-1.8411	232.1	0.7892	< 2.2e-16

579 Note: F-statistic degrees of freedom for Greenhouse Experiment 1 were 1,54 and were 1,62 for Greenhouse Experiment 2

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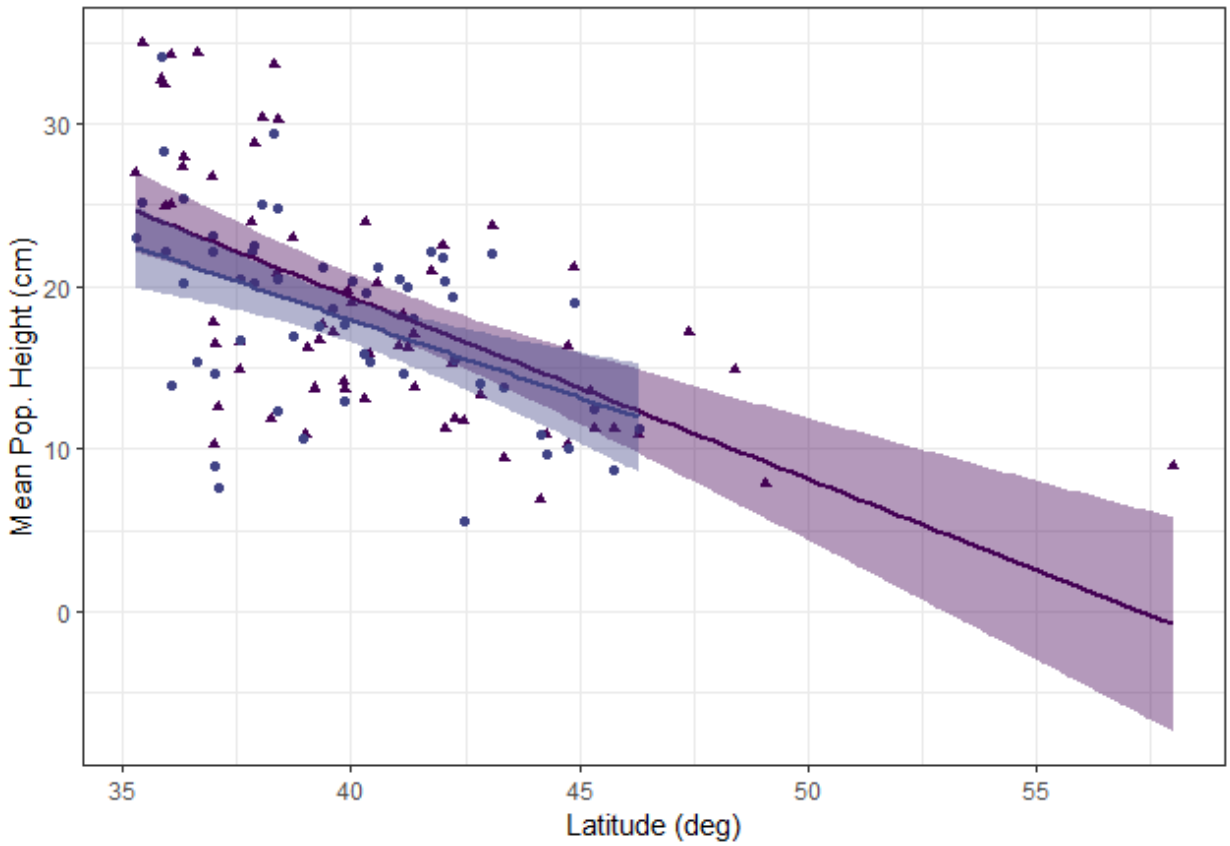
588 **FIGURES**



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590 **Figure 1.** Linear regression of the relationship between latitude of origin for *M. guttatus*
591 populations and the average heights of individuals of these populations grown in the
592 greenhouses. Indigo circle points represent populations raised in Greenhouse 1, and purple
593 triangle points represent populations raised in Greenhouse 2. Both regressions are statistically
594 significant ($p < 0.01$).

595

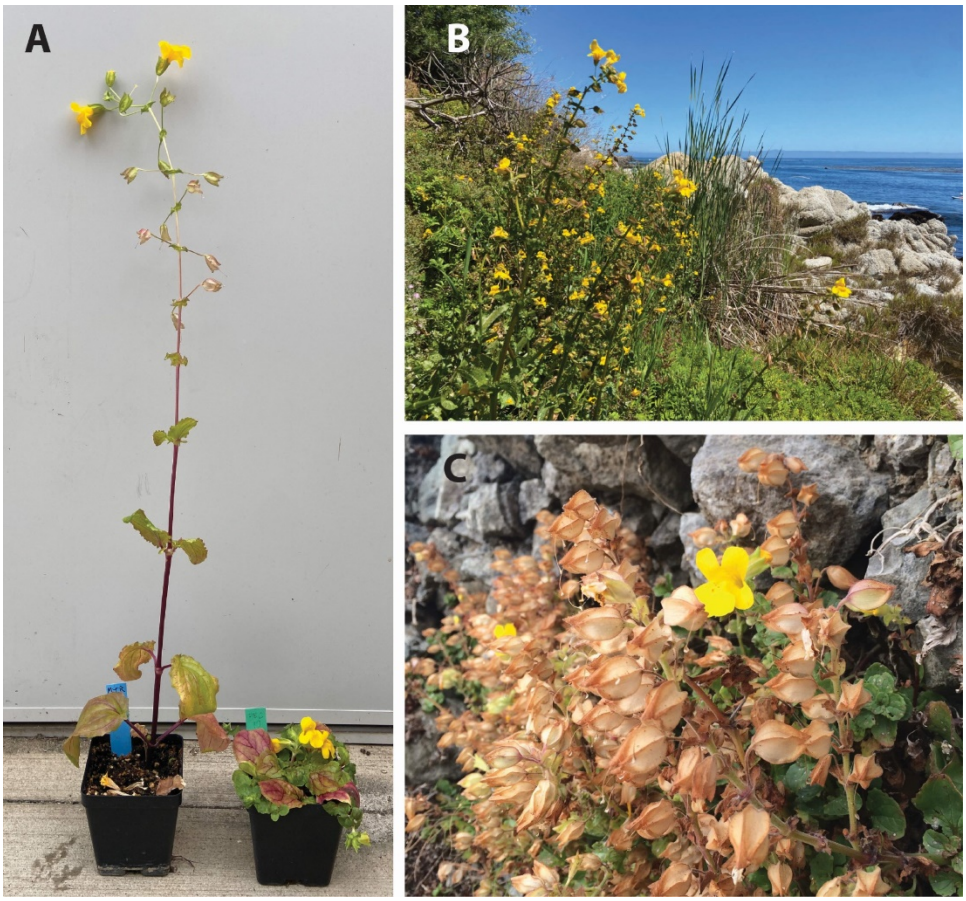

Figure 2. Variation in plant height in *Mimulus guttatus.* A) Divergence in height between plants from the Central California coast (left) and Oregon (right) when grown in a greenhouse common garden experiment. B) Tall plants growing along the Central California coast reach up to 2 meters in height. C) Plants growing along the coast in Oregon are more compact in growth form.

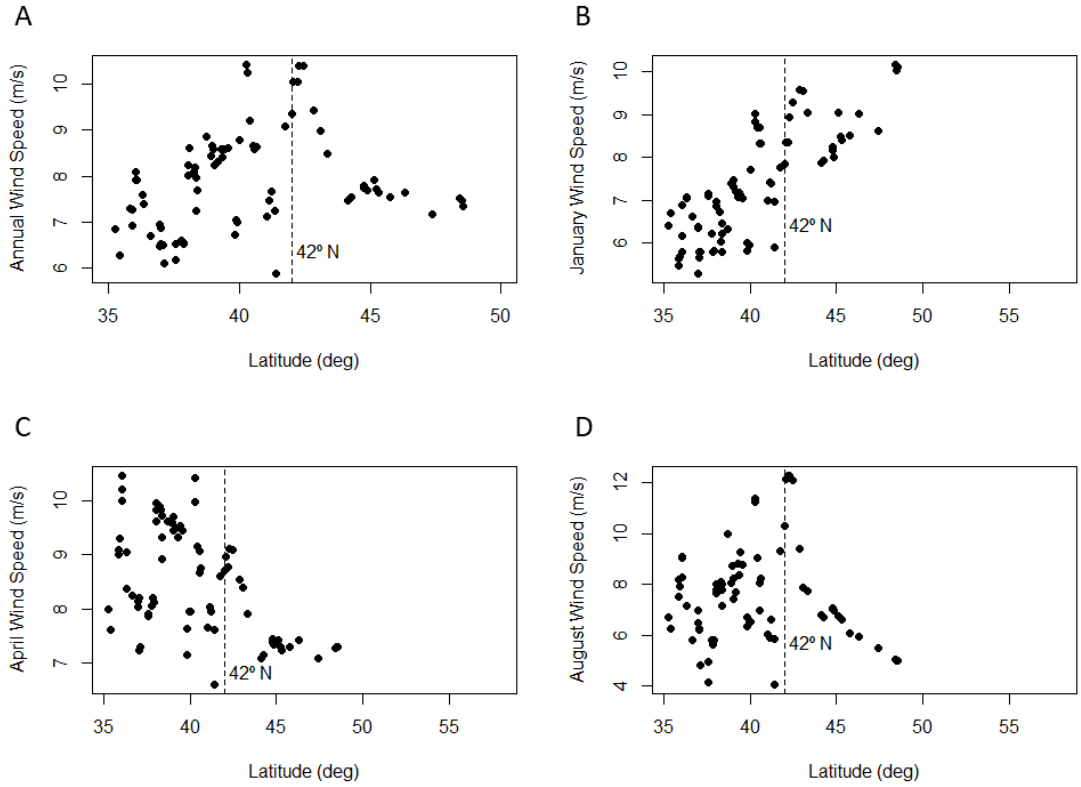

Figure 3. Mean wind speeds (m/s) along the United States Pacific Coast reported annually (A), during January (B), April (C), and August (D). The dashed line indicates 42° N, the latitude of the Oregon coast at which wind speeds start declining going further north.

SUPPLEMENTARY MATERIAL

Table S1. Principal Component Loadings and Coordinates for Greenhouse Experiment 1

Climate Variables	PC1 loading	PC2 loading	PC3 loading	PC4 loading	PC1 coordinate	PC2 coordinate	PC3 coordinate	PC4 coordinate
Q1Wind	4.7449265	3.8933108	1.8929443	0.0074429	0.8198760	-0.4276365	0.2248873	0.0092769
Q2Wind	0.0124223	2.3409782	29.7008855	0.0484955	-0.0419502	-0.3315995	0.8908012	0.0236802
Q3Wind	1.7739690	3.3327906	17.7481881	0.0103884	0.5013101	-0.3956574	0.6886096	-0.0109600
Q4Wind	5.2802762	3.1766903	1.0233375	0.0205459	0.8648917	-0.3862804	0.1653505	-0.0154133
WindAnnual	2.5906409	4.4450227	15.2435472	0.0000002	0.6058108	-0.4569327	0.6381740	-0.0000490
AnnTemp	6.3433504	0.2197840	0.0108660	4.1278805	-0.9479660	-0.1016046	-0.0170385	-0.2184728
DiurnalRange	3.4968500	4.8877912	5.3021721	9.5279702	-0.7038367	0.4791501	0.3763769	0.3319204
Isothermality	3.8984923	2.2127317	1.8480043	18.1269951	-0.7431590	-0.3223886	0.2222018	0.4578221
TempSeasonality	0.4632877	17.6388953	1.7888015	3.7936280	0.2561880	0.9102296	0.2186136	-0.2094407
MaxTemp_WarmMonth	3.9263041	7.0925750	3.3380579	0.3554186	-0.7458051	0.5771879	0.2986366	-0.0641068
MinTemp_ColdMonth	1.1783690	11.6069940	2.2681721	17.6298756	-0.4085771	-0.7383718	-0.2461694	-0.4515007
TempAnnRange	1.4526542	13.6196131	4.7440718	1.6514689	-0.4536433	0.7998299	0.3560178	0.1381876
TempWetQuarter	4.7505953	5.7312285	0.0955002	1.3391414	-0.8203656	-0.5188468	-0.0505124	-0.1244363
TempDryQuarter	3.9910093	4.8960362	1.1994531	11.2226697	-0.7519254	0.4795540	0.1790143	-0.3602317
TempWarmQuarter	4.4405749	3.9872096	0.6432115	10.3684736	-0.7931458	0.4327627	0.1310910	-0.3462511
TempColdQuarter	5.0049115	4.8110737	0.2660906	0.6330349	-0.8420378	-0.4753749	-0.0843162	-0.0855554
AnnPrecip	6.5362397	0.4393174	0.3745736	2.2974578	0.9622710	0.1436496	0.1000379	-0.1629887
PrecipWetMonth	5.9663180	0.4246475	1.0996666	5.9058571	0.9193621	0.1412308	0.1714062	-0.2613216
PrecipDryMonth	4.4475359	2.0116984	4.3691156	1.9567445	0.7937672	0.3073949	-0.3416590	0.1504184
PrecipSeasonality	5.9642127	0.3193915	1.0051339	1.2306553	-0.9191999	-0.1224833	0.1638732	-0.1192894
PrecipWetQuarter	6.2284665	0.4230799	0.9455099	4.0132959	0.9393425	0.1409699	0.1589385	-0.2154192
PrecipDryQuarter	5.5609895	1.1543451	2.3090199	0.4665059	0.8875840	0.2328537	-0.2483762	0.0734450
PrecipWarmQuarter	5.8628034	0.9038088	1.5353738	0.4709767	0.9113518	0.2060409	-0.2025364	0.0737961
PrecipColdQuarter	6.0848009	0.4309863	1.2483029	4.7950773	0.9284459	0.1422810	0.1826233	-0.2354678

Table S2. Principal Component Loadings and Coordinates for Greenhouse Experiment 2

Climate Variables	PC1 loading	PC2 loading	PC3 loading	PC4 loading	PC5 loading	PC6 loading	PC1 coordinate	PC2 coordinate	PC3 coordinate	PC4 coordinate	PC5 coordinate	PC6 coordinate
Q1Wind	4.3843848	3.2314270	2.4502873	0.7983780	1.8765040	22.3732323	0.7671537	0.4217511	-0.2529117	-0.0861679	-0.1091620	0.3333754
Q2Wind	0.3768277	3.6407226	24.8838252	1.0983227	1.9832131	2.7193330	-0.2249052	0.4476647	-0.8059702	-0.1010662	-0.1122229	-0.1162252
Q3Wind	0.8635182	5.4417680	18.1054543	0.0104486	12.0414096	0.4329545	0.3404582	0.5473046	-0.6874880	0.0098576	0.2765257	0.0463757
Q4Wind	5.1450571	3.1904171	1.4492831	0.0179842	0.0047425	12.2987882	0.8310424	0.4190664	-0.1945078	-0.0129326	0.0054878	0.2471726
WindAnnual	1.5963802	6.0948328	16.4460761	0.2694635	0.5216136	2.9070556	0.4629097	0.5792152	-0.6552266	-0.0500600	0.0575534	0.1201699
AnnTemp	6.7184529	0.1776023	0.0038761	5.3058906	4.8884824	0.5609606	-0.9496481	0.0988743	-0.0100591	0.2221366	0.1761911	0.0527880
DiurnalRange	3.7500835	3.9658549	4.8549101	9.5173513	5.1346629	3.5233552	-0.7094937	-0.4672265	-0.3560008	-0.2975083	0.1805730	-0.1322962
Isothermality	4.4205587	3.2689307	0.4681782	9.9016747	8.4104450	8.6835226	-0.7703120	0.4241915	-0.1105518	-0.3034557	0.2311034	-0.2076907
TempSeasonality	0.9537103	14.0636287	2.4165093	0.8244544	1.0626286	3.1155190	0.3577967	-0.8798482	-0.2511624	0.0875637	-0.0821462	0.1244040
MaxTemp_WarmMonth	3.0383943	8.3455266	4.4200214	0.2976827	0.5112156	0.1636737	-0.6386312	-0.6777756	-0.3396820	0.0526160	0.0569769	0.0285140
MinTemp_ColdMonth	1.6368959	9.7506077	1.5771838	20.1062109	0.3569091	0.3101932	-0.4687471	0.7326135	0.2029091	0.4324203	0.0476075	0.0392541
TempAnnRange	0.7308812	13.5203534	5.0073569	2.2282360	0.1019958	0.0074547	-0.3132214	-0.8626867	-0.3615469	-0.1439533	0.0254500	0.0060853
TempWetQuarter	4.8660637	5.2473663	0.1227338	2.2123170	3.8769347	0.1526979	-0.8081965	0.5374397	0.0566034	0.1434381	0.1569066	-0.0275414
TempDryQuarter	3.1071548	6.8505531	2.8384888	9.7881553	1.7452617	4.8230355	-0.6458171	-0.6140757	-0.2722099	0.3017112	0.1052755	0.1547852
TempWarmQuarter	3.6982025	5.7268566	1.9385112	10.3630140	3.2066364	3.6991858	-0.7045688	-0.5614579	-0.2249544	0.3104445	0.1426993	0.1355571
TempColdQuarter	5.1383409	4.4257274	0.2993206	1.7181994	5.6880054	0.0814673	-0.8304998	0.4935730	0.0883952	0.1264089	0.1900539	-0.0201169
AnnPrecip	6.7487340	0.1245649	0.7205310	3.5171208	0.3414570	6.0570145	0.9517858	-0.0828051	-0.1371471	0.1808567	0.0465656	-0.1734597
PrecipWetMonth	6.1215200	0.1188437	1.7608788	7.8431993	0.0643518	8.7286477	0.9064789	-0.0808811	-0.2144002	0.2700770	-0.0202152	-0.2082297
PrecipDryMonth	5.1432074	1.3473748	3.1582917	1.2706166	15.4562933	1.6896000	0.8308930	-0.2723349	0.2871353	-0.1087047	0.3132922	0.0916138
PrecipSeasonality	6.4834833	0.1558699	0.8209399	0.8501078	5.4040727	0.3903922	-0.9328939	0.0926276	-0.1463916	0.0889156	-0.1852497	-0.0440372
PrecipWetQuarter	6.3767695	0.1285835	1.5239047	5.5203626	0.0170095	8.1894952	0.9251847	-0.0841301	-0.1994524	0.2265817	-0.0103930	-0.2016962
PrecipDryQuarter	6.1080873	0.5747741	1.6439590	0.0523528	15.6983277	0.0274041	0.9054838	-0.1778720	0.2071600	-0.0220654	0.3157356	0.0116675
PrecipWarmQuarter	6.4077079	0.4915632	1.1108009	0.0590273	11.4423299	0.0083199	0.9274263	-0.1644935	0.1702858	-0.0234297	0.2695591	-0.0064288
PrecipColdQuarter	6.1855840	0.1162509	1.9786777	6.4294294	0.1654978	9.0566975	0.9112099	-0.0799940	-0.2272730	0.2445272	-0.0324185	-0.2121066

Table S3. *M. guttatus* population codes and coordinates

PopCode	Latitude	Longitude
ALA	58.00433	-135.743
BCB	36.06285	-121.592
BHE	38.30703	-123.058
BLN	42.83772	-124.56
BND	43.07971	-124.43
BON	37.00016	-122.182
BRK	42.06429	-124.301
BYR	43.34902	-124.346
CAB	39.3592	-123.817
CKI	45.24213	-123.969
CMD	40.40923	-124.392
CML	41.04636	-124.123
COV	40.02157	-124.069
CPT	36.9746	-121.945
CRD	36.30686	-121.85
CRU	35.84372	-121.404
CVG	38.3723	-123.055
DAV	37.02498	-122.218
DIL	38.25167	-122.968
DIS	46.3053	-124.072
FPT	37.80918	-122.475
FRA	39.0083	-123.694
GBM	41.37863	-124.07
GRE	37.07795	-122.268
GRZ	40.56885	-124.212
GWC	37.56394	-122.514
HEC	44.13536	-124.124
HOC	47.3854	-123.147
HUM	39.92726	-123.761
LAG	41.23157	-124.106
LBG	49.07185	-125.768
LJA	39.86053	-123.902
LOK	45.33825	-123.977
MTO	40.28343	-124.36
MTR	37.5517	-122.514
MXX	40.31068	-124.267
NAV	39.1869	-123.757
OPB	42.46402	-124.423
ORO	35.27335	-120.889
OSW	45.76108	-123.967
OTT	44.75224	-124.064
PCR	41.39856	-124.069
PGR	36.62799	-121.921
PPT	41.13709	-124.152
PTL	42.28225	-124.405
PTR	38.04861	-122.869
PTU	44.27916	-124.112
PUN	44.74484	-124.06
SCC	48.41262	-124.012
SDB	35.92127	-121.467
SIM	44.87659	-124.038
SRN	38.72593	-123.481
STB	37.89132	-122.635
SUR	36.33194	-121.889
SWB	39.03598	-123.691
TSU	41.75983	-124.222
USB	39.83218	-123.849
VIC	36.04834	-121.589
WCK	42.00256	-124.213
WCR	35.89838	-121.461
WEV	35.42313	-120.789
WOD	39.31239	-123.803
WPT	42.21213	-124.377
WPV	39.59383	-123.785
WSZ	36.96233	-122.076
WTB	38.40525	-123.096
CVR	38.3684	-123.061
MUR	37.87685	-122.558
OZF	38.95578	-123.66