One of the most fundamental premises in the study of plant/herbivore interactions is the idea of allocational tradeoffs between plant growth and plant defense (Herms and Mattson 1992). The theory of growth/defense tradeoffs is commonly tested by measuring variation in plant defenses across gradients of resource availability (Coley et al. 1985). For example, Fine et al. (2006) showed that plant species from nutrient-poor white sand sites in the Amazon grow slowly but are highly resistant to herbivores, whereas close relatives from clay sites grow quickly but are susceptible to herbivores.

An alternative approach to measuring growth/defense tradeoffs along gradients of resource availability is to instead compare across gradients of herbivory intensity. Examples of this approach include comparative studies that find reductions in defensive traits in plants at higher latitudes (references) and higher elevations (references), with the idea that pressure from herbivores is more intense in the tropics and at lower elevations. Studies that experimentally limit herbivory also often find evidence for reduced investment in defense traits. For example, Palmer et al. (2008) showed that excluding large mammalian herbivores led to the breakdown of ant-acacia defense mutualisms, and Agrawal et al. (2012) found that multi-year insecticide treatment was associated with evolution of increased competitive ability in evening primrose.

One commonly-studied contrast involves focusing on defensive traits in plants from oceanic islands and their mainland relatives. These contrasts are most informative when islands are missing entire assemblages of herbivores—particularly large mammalian herbivores—and their constituent floras have evolved in isolation for extended periods. Numerous studies have used either conspecific or congeneric comparisons of island and mainland taxa and found reduced expression of putative defense traits on islands (Bowen and Van Vuren 1997, Vourc’h et al. 2001), and many studies have also noted that plants from oceanic islands are especially susceptible to the effects of introduced mammalian herbivores. One of the best-cited examples of defense trait reduction on islands is Bowen and Van Vuren (1997), which compared island and mainland plant traits for six taxonomic pairings from Santa Cruz Island and the California mainland and also showed increased palatability of island taxa in choice tests using domesticated sheep.

A recent meta-analysis of studies comparing island and mainland plants found evidence for increased mammalian herbivore damage in island compared to mainland plants, supporting the idea that island plants may be more susceptible to introduced mammalian herbivores (Moreira et al. 2020). However, somewhat surprisingly, this meta-analysis did not find consistent evidence for reductions in plant defensive traits on islands across a set of 173 cases of island/mainland comparisons. Thus, the degree to which island plants show reduced defense traits remains an open question. Reasons for the lack of reduced defensive trait expression in island plants are numerous but might include (i) recent introduction of non-native mammalian herbivores that select for increased defensive traits, either through phenotypic plasticity or directional selection; (ii) selection by invertebrate herbivores that are less dispersal-limited and may be equally (or even more) abundant on islands; (iii) ongoing gene flow from mainland populations that limits the degree of differentiation in island populations.

Even in instances where studies do find evidence for reductions in plant defensive traits on islands, methodological drawbacks may limit the scope of these conclusions. First, many studies only include comparisons from a single conspecific or congeneric pair, and likewise, measurements may only contrast a single island and single mainland site. Thus, it is often unclear whether trait divergence between islands and mainland plants are the product of adaptive divergence or idiosyncrasy. Second, few studies have attempted to measure plant traits from island and mainland genotypes grow under common environmental conditions, thereby raising the possibility that trait divergence is the result of differences in the abiotic environment between island and mainland sampling locations. Third, traits that are assumed to be defenses against herbivores may be have alternative functions and be maintained in island plants (e.g. phenolic compounds that provide UV resistance). Finally, and related to the third point, comparatively few studies functionally verify the importance of putative defensive traits using experiments with herbivores.

In this paper, we attempt to address some of these shortcomings through two studies comparing plant populations from the California Channel Islands and nearby mainland locations. In the first study, we used five taxonomic pairs of woody chaparral shrubs sampled across three island and three mainland sites, as well as two mainland common garden locations, to test for divergence in leaf area, specific leaf area, marginal leaf spinescence, and concentrations of cyanogenic glycosides. In the second study, we collected 44 genotypes of California hedgenettle (*Stachys bullata*: Lamiaceae) from two island and four mainland locations and grew them for two years in a mainland common garden to measure plant chemistry and growth. In general, we do find evidence for reductions in putatively defensive traits in island plants, although the magnitude of these effects differs across species and islands.

**Methods**

Background – California Channel Islands

The California Channel Islands are a group of uplifted volcanic oceanic islands off the coast of southern California that arose over the past 5 million years (Pinter et al. 1998, [NPS](https://www.nps.gov/chis/learn/nature/geologicformations.htm)), ranging in size from 2.6 km2 (Santa Barbara Island) to 249 km2 (Santa Cruz Island) land area. The northern Channel Islands (including Santa Cruz and Santa Rosa) were periodically connected as a single landmass (Santa Rosae) during Pleistocene Ice Ages (Kennett et al. 2008), with as little as 5 miles of separation between island and mainland. The southern Channel Islands (including Santa Catalina) are generally more isolated from each other and the California mainland. Large mammalian herbivores have historically been absent from the California Channel Islands—with the notable exception of the pygmy mammoth (*Mammathus exilis*) (Agenbroad 2012)—but were introduced by Europeans in the 1800s (Table Sxx). In the last 50 years, concerted eradication efforts have removed large mammals from Santa Cruz and Santa Rosa Island; mule deer and American bison are still present on Catalina Island. The Channel Islands flora has a high degree of endemism and features many examples of insular woodiness and island gigantism (Guilliams et al. 2017).

Chaparral shrub sampling

We selected six pairs of taxa characteristic of the chaparral plant community that occur on both the California Channel Islands and the nearby southern California mainland. Pairs were chosen to match those in Bowen and Van Vuren (1997) and consisted of either congeners or conspecifics (Figure 1B) from three plants families: Rosaceae (*Cercocarpus*, *Prunus*, *Heteromeles*), Papaveraceae (*Dendromecon*), and Rhamnaceae (*Ceanothus*). One species pair (*Quercus pacifica*, *Q. berberidifolia*) was collected but not included in subsequent analyses, since phylogenetic evidence published after Bowen and Van Vuren (1997) has shown that these taxa are not sister species and diverged in the Miocene (>5.3 mya) (Hipp et al. 2020). For the remaining five taxonomic pairs, we did reconnaissance trips to each collection site in 2015 and noted the location of taxa using a handheld GPS. We then returned to these locations in February and March of 2016 to collect leaf tissue for use in morphological and chemical analysis. In total, we sampled 291 individual plants from five taxonomic pairs across six sites (three island, three mainland), for an average of approximately 10 plants per site (Figure 1). Hereafter, we refer to taxonomic pairs as “species pairs” for brevity, even in the case of congeners.

We collected leaf tissue for morphological analysis from focal plants by clipping branches containing variable numbers of leaves. When possible, we collected a branch from both the lower (<1 m in height) and the upper (>2 m in height) portion of the plant canopy to capture morphological differences associated with accessibility to mammalian herbivores. For analysis of cyanogenic glycosides, we collected individual leaves from the lower portion of the plant canopy for three species (*Heteromeles*, *Prunus*, *Cercocarpus*), and when possible, included both fully mature/expanded leaf tissue as well as young/actively expanding leaf tissue. Leaf chemistry samples were immediately frozen on dry ice and were later transferred to a -80C freezer until processing. For each sampled plant, we recorded its GPS coordinates (see Supplemental Figure xx), elevation, and slope aspect (when relevant) using a handheld Garmin GPS device, and we also recorded the approximate stem diameter at 0.25m above the ground using a digital caliper.

For each sampled branch, leaves were removed and imaged using a flatbed scanner with a scalebar. We recorded the following measurements from each leaf: total area (including petiole), area and length (not including petiole), percent of leaf tissue missing due to herbivory, and marginal leaf spinescence. All measurements were taken using ImageJ v 1.51 (Schneider et al. 2012). For a visual depiction of our measurement protocol, see Supplemental Figure xx. Non-fully expanded leaves (n = 809) were measured but were excluded from subsequent analyses. We also measured specific leaf area (SLA) at the level of branches by taking the cumulative area of all fully expanded leaves (in cm2) and dividing this by their cumulative mass (in g).

To measure cyanogenic glycoside (CNglc) content, we followed a modified version of the evolved hydrogen cyanide (HCN) protocol described in Experiment 2 of Gleadow et al. (2012). We only collected tissue for species in the Rosaceae (*Cercocarpus*, *Heteromeles*, *Prunus*), which are known to produce CNglcs. A piece of fresh, frozen leaf tissue was massed, transferred to a 1.5 mL tube with magnetic grinding beads, added to liquid nitrogen, and pulverized in a tissue lyser (info) at 50 Hz for 30 seconds total. Next, we added 1 ml of 0.1M citrate buffer to each tube containing ground frozen tissue, which was then transferred into a larger 15 mL tube containing a separate 1.5 mL tube with 1 ml of 1M NaOH. This larger 15 mL tube was sealed, allowed to incubate at room temperature for 1 hour, and then transferred into a 37C chamber to incubate for 12 hours overnight. The amount of NaCN captured in NaOH was measured via the pyridine-pyrazolone method using reagents purchased from Hanna Insruments (HI93714-01). The 1 mL of dissolved NaCN was added to 30 mL of deionized water and neutralized with 0.5M acetic acid. We then added 1 mL of this solution to a separate container of 10 mL of deionized water and added reagents A, B, and C according to manufacturer instructions. The resulting color change (from clear to blue) was measured in a plastic cuvet inserted into a spectrometer (info), with absorbance was measured at 595 nm. This absorbance value was then compared to a calibration curve prepared using known concentrations of KCN (Supplemental Figure xx) to obtain a sample concentration. We also experimentally added 0.5 mg of beta-glucosidase (Sigma Aldrich) to a small subset (n = 3) of tissue samples in citrate buffer to test whether endogenous enzyme activity was sufficient to hydrolyze all cyanogenic glycosides; this addition did not appreciably change the resulting absorbance values. In total, we generated 194 measurements of CNglc content from 80 individual plants.

Because most of our leaf tissue sampling was conducted *in situ* (i.e. from plants growing in their native environment), it is therefore difficult to know whether any potential phenotypic differentiation between island and mainland plants is environmentally or genetically determined.Thus, we also sampled leaf tissue from two botanical gardens (Santa Barbara Botanic Garden and Rancho Santa Ana Botanic Garden) on the mainland that featured island and mainland genotypes of the species of interest (Supplemental Figure xx), grown from either seed or cuttings. All leaf tissue collection, morphological analysis, and chemical analysis was conducted in the same way as described above, although SLA was not measured for common garden plants. In total, we sampled an additional 40 plants (18 island and 22 mainland genotypes) from these common garden environments (Supplemental Figure xx).

Finally, we also took advantage of a series of herbivore exclosures on Catalina Island—which still has introduced deer and bison present—to test for the potential effects of herbivore-mediated plasticity in plant traits. Because of the small number of exclosures available, our sampling across species was somewhat uneven, though we were still able to sample a total of 24 plants inside of exclosures and 35 plants outside of exclosures (Supplemental Table xx). To the extent possible, we attempted to sample plants outside of exclosures that were nearby to those inside exclosures to minimize fine-scale environmental effects on leaf morphology and chemistry.

Chaparral shrubs – statistical analyses

We analyzed our data using multilevel linear mixed models implemented in the lme4 package (Bates et al. 2015) in R version 3.6.3 (R Core Development Team) to account for the highly hierarchical nature of our data. Response variables of interest were leaf area, specific leaf area, marginal leaf spinescence, and leaf CNglc content. In all cases, response variables were analyzed as untransformed values with a normal error distribution. For marginal leaf spinescence, we only included *Heteromeles* and *Prunus*, since these were the only species with stiff rigid spines. Likewise, CNglc levels in *Cercocarpus* were ~100x lower than in *Prunus* and *Heteromeles* (and often below our detection limit), so CNglc analysis was restricted to the latter two species. Fixed covariates that were included in each model included site of collection, canopy position (upper versus lower), north/south slope aspect, and east/west slope aspect. We considered including elevation and stem diameter (as a proxy for plant age) as covariates, though because of limited within-site and within-species variation in these measures, we ultimately omitted them from analyses.

For each response variable, we started by fitting an overall model that included all samples collected *in situ* across all species (n = 4096 leaves from 291 plants). These models were of the form (in lme4 syntax):

***Response variable ~ IM + (IM|Species) + covariates + (1|Plant.ID/Branch.ID)***

where IM corresponds to whether samples came from an island or mainland site. Plant species is included as a random intercept, with a random slope for island vs. mainland status to allow for variation in the magnitude of the island/mainland contrast across species. Each individual plant receives its own random intercept, and finally, each branch (upper versus lower) gets its own random intercept nested within plant ID. Since specific leaf area was calculated by pooling leaves from within branches, the SLA model does not include a branch ID term. In these overall models, the primary contrast of interest is the fixed effect of island/mainland, which reflects the average of the five species-level island/mainland contrasts.

For two of the response variables (marginal spinescence, CNglc content), we included additional parameters based on *a priori* hypotheses. In the model considering marginal spinescence, we included an interaction between island/mainland status and canopy position to allow for the degree of spinescence heteroblasty to vary across environments (e.g. Burns 2014). In the model considering CNglc content, we included a term for leaf age (old vs. young) based on our sampling scheme and predictions from optimal plant defense theory that younger leaf tissue should be more heavily defended against herbivores (Herms and Mattson 1992).

Next, to understand variation among species in the degree of island/mainland trait divergence, we ran separate models for each species that were identical to the models specified above, but without the (IM|Species) term. These models allowed us to generate species-specific estimates of the island/mainland effect, which may be important given the heterogeneity in degree of evolutionary divergence among our taxonomic pairs. We report both the overall models and the species-level models together for each response variable for comparison.

To test for genetically based differences in trait values, we analyzed samples collected from common garden samples in a separate set of linear mixed models. These models were similar to those described above and were of the form:

***Response variable ~ Source.IM + (Source.IM|Species) + covariates (1|Plant.ID/Branch.ID)***

where Source.IM refers to whether the plants’ original provenance was an island or mainland location. As above, we also separately generated species-specific estimates of the island/mainland effect for samples collected from common garden locations.

Finally, to test for the effect of access to introduced herbivores on Catalina Island, we analyzed all trait data from Catalina and included a term to account for whether samples came from inside versus outside of an herbivore exclosure.

For all models evaluated, their output was generated using the lmerTest package (Kuznetsova et al. 2017), which gives approximate degree of freedom and p-value calculations. Comparisons across factor levels were generated using emmeans version 1.5.3 (Lenth 2020). Raw data were plotted using ggplot2 (Wickham 2016).

*Stachys bullata* – background

*Stachys bullata* (Lamiaceae) is a perennial herbaceous plant that occurs in coastal California from approximately Orange County to the San Francisco Bay Area, with populations present on Santa Cruz, Santa Rosa, and Anacapa Islands. It reproduces both clonally via rhizomes and sexually and is described as being glandular, with aromatic foliage that is characteristic of many plants in the Lamiaceae. However, island populations have been noted to have non-aromatic foliage as well as larger leaves and flowers than their mainland relatives (Junak et al. 1995), and densities of glandular trichomes appear to be much lower on island plants (Figure 3C).

*Stachys bullata* common garden experiment

To determine whether the reduction in aromaticity and glandular trichomes is environmentally or genetically determined, we set up a multi-year common garden experiment where we grew island and mainland *S. bullata* genotypes together at the Santa Barbara Botanic Garden (SBBG). Plants were collected in the field in late 2015 from two island (Santa Cruz, Santa Rosa) and four mainland locations (Figure 3A) as rhizomes, which were transported to UC Davis and shallowly planted in potting mix. Plants were grown in 1 gallon pots for approximately three months and were then split into clonal replicates that were grown in their own 1 gallon pots. In total, we collected 44 S*. bullata* genotypes that were separated into 112 individual plants (Figure 3B).

In February 2016, we set up a common garden plot at the SBBG (Figure 3D). The plot was located on an east-facing slope that received partial or full sun throughout the year. Plants were spaced at a distance 1 m apart from each other in a gridded pattern. The plot was surrounded by a 2 m fence to prevent browsing by deer, and each plant was enclosed in a cage made from hardware cloth to limit root herbivory by pocket gophers (*Thomomys bottae*), which were common at the site. We installed a drip irrigation system to assist with initial plant establishment. Plants were randomly outplanted in late February and early March of 2016, and received approximately 2L of water at 1 week intervals between March-August 2016. At this point, we ceased supplemental watering, and plants subsequently only received natural precipitation. Plants became dormant in September 2016, and then subsequently began to regrow naturally in February 2017. In addition, we set up a smaller common garden at the Santa Cruz Island Reserve, although due to concerns over introduction of non-native genotypes, this common garden consisted of only genotypes from Santa Cruz Island.

We collected two categories of data from common garden *Stachys bullata*. First, we measured annual growth by collecting all above-ground biomass at the end of the growing season and recording its mass. Biomass measurements were collected in both 2016 and 2017. Second, we also measured plant secondary chemistry—with an emphasis on volatile organic compounds present on leaf surfaces and in glandular trichomes—using a modified version of the protocol described in Pratt et al. (2014) for measuring terpenes in *Artemisia californica*. Briefly, in April of 2017, we used a hole punch to collect six leaf discs, each from a different leaf, from approximately 75 *Stachys* plants across all genotypes. This plant tissue was added to 2 mL glass vials containing 500 uL of dichloromethane and 5 uL of a 90 ng/ml tetralin internal standard and was stored at 4C until processing. Vials were sonicated for 10 minutes, and then 200 uL of the eluent was filtered through a modified capillary tube containing powdered silica into a GCMS vial insert. Samples were injected onto an Agilent 7890B gas chromatograph fitted with a 30 m × 0.25 mm × 0.25 um HP‐5 Ultra Inert column coupled to an Agilent 5977A mass spectrometer (Agilent Technologies) using a 5:1 split ratio, a 1 uL injection volume, and an inlet temperature of 250C. The initial oven temperature was 40°C, held for 3 minutes, followed by a temperature ramp of 5°C/min up to 210°C, followed by a subsequent ramp of 20°C/min to 300°C, followed by a final hold at 300°C for one minute. Helium was used as the carrier gas at a flow rate of 1.2 mL/min. Electron impact mass spectra were obtained by scanning between 30-550 *m/z*.

GC/MS data were processed using MassHunter GC/MS Acquisition software version B.07.00 and MSD ChemStation Enhanced Data Analysis Software version F.01.00 (Agilent). Peaks were initially called automatically using the RTE integrator and a detection threshold limit of 1.0% of the largest peak. Chromatograms were manually annotated to include peaks that were visible but fell below this detection threshold. Peak alignment was based on retention times, and we assigned identifications to compounds by comparing mass spectra and retention times to published databases (Adams 2007, NIST mass spectral library). In total, our dataset included peaks from 79 unique retention times.

*Stachys* data analysis

We analyzed aboveground biomass using a linear-mixed effects model of the form:

***Aboveground biomass ~ IM + Year + (1|Source.Pop/Genotype) + (1|Column) + (1|Row)***

where IM refers to whether a given plant originated from an island or mainland site and column and row refer to the location of plants within the common garden grid.

To analyze plant chemistry, we divided each integrated peak area by its corresponding internal standard peak area to standardize all values. We added all peaks together to get a cumulative compound abundance measure and also separated compounds based on their biochemical basis (i.e. fatty acid derivatives, mono- and sesquiterpenes, aromatics). To visualize multivariate disparity among populations in chemical composition, we used non-metric multidimensional scaling (nMDS) implemented in the vegan package version 2.5-7 (Oksanen et al. 2020), specifying Bray-Curtis distances, k = 8 dimensions, and 1000 random starts in the metaMDS function; group-level differences between genotypes from island versus mainland sites were assessed using perMANOVA implemented via the adonis2 function in vegan (Oksanen et al. 2020). We also separately tested for multivariate disparity using only genotypes collected from mainland sites, as well as Santa Cruz Island genotypes grown on Santa Cruz Island versus the mainland.

**Results**

Chaparral shrubs

In our overall models of island/mainland differentiation, none of the traits we measured resulted in significant differences between island and mainland species. That said, all effect sizes were in the predicted direction: overall, island plants had larger leaves (t = 2.398, p = 0.073), lower specific leaf area (stats), reduced marginal spinescence (stats), and lower concentrations of CNglcs (stats).

In the overall model for leaf area, island plants had leaves that were, on average, 44.5% larger than their mainland relatives (x̄isl = 7.66, x̄main = 4.25). Leaves from the upper canopy were modestly smaller than leaves from lower in the canopy (t =  -1.711, p = 0.088). For within-species comparisons of leaf area, two species pairs had significantly larger leaves on islands: *Ceanothus* (t = 3.853, p = 0.013) and *Prunus* (t = 4.126, p = 0.015) (Table xx). Among common garden plants, island genotypes had leaves that were, on average, 36.6% larger than their mainland relatives (x̄isl = 10.72, x̄main = 6.79), although the island/mainland contrast was not significant in the overall model (t = 3.925, p = 0.239). For within-species comparisons of common garden leaf area, *Prunus* genotypes from islands had significantly larger leaves than mainland genotypes (t = 4.880, p = 0.001).

In the overall model for specific leaf area, island plants had SLA that was, on average, 13.5% higher than for mainland plants (x̄isl = 6.53, x̄main = 5.65), indicating thinner leaves for island genotypes, although the island/mainland difference was not significant in the overall model for plants sampled in situ (t = 1.794, p = 0.135). Leaves from the upper canopy had consistently lower SLA (t = -6.661, p < 0.001), as did leaves from plants with northward (t = 3.248, p = 0.001) and westward facing aspects (t = 3.076, p = 0.002). None of the species-level island/mainland contrasts resulted in significant island/mainland contrasts (Table xx). SLA was not measured for plants from common gardens.

In the overall model for marginal leaf spinescence, island plants had spines that were, on average, reduced by 67.4% compared to mainland plants (x̄isl = 10.72, x̄main = 6.79), but the overall island/mainland difference was not significant (t = 1.887, 0.279) due to the small number of species (n = 2) included in the analysis. Leaves from the upper canopy had consistently reduced spinescence (i.e. spinescence heteroblasty) (t = -2.028, p = 0.045), and there was a significant interaction between island/mainland status and canopy position (t = 2.826, p = 0.006) that reflects more pronounced spinescence heteroblasty in mainland plants. Within species, marginal spines were significantly reduced on islands for both Heteromeles (t = -3.063, p = 0.034) and Prunus (t = 8.008, p < 0.001). Among common garden plants, within species comparisons of marginal spines were similar to those from plants measured in situ, with modestly reduced spines in island Heteromeles (t = -1.952, p = 0.094) and significantly reduced spines in island Prunus (t = 8.597, p < 0.001) (Table xx).

In the overall model for CNglc content, island plants had, on average, 40.2% lower CNglc concentrations than their mainland relatives (x̄isl = 1.31, x̄main = 2.19), though as with marginal leaf spinescence, the overall island/mainland difference was not significant (t = 2.392, p = 0.154) because only two species were sampled for this analysis. Younger leaf tissue had consistently higher CNglc content than older, fully expanded leaf tissue, regardless of plant provenance (t = 5.364, p < 0.001). Within species, CNglc concentrations were lower for Heteromeles (t = -2.430, p = 0.055) and significantly lower for Prunus (t = -3.353, p = 0.015). Among common garden plants, within species comparisons of CNglc concentrations were similar to those from plants measured in situ but with a smaller island/mainland effect, with modestly reduced concentrations in Heteromeles (t = -1.316, p = 0.213) and significantly reduced concentrations in Prunus (t = -2.389, p = 0.036).

Finally, we did not find any significant differences for any measured traits inside versus outside of herbivore exclosures on Catalina Island (Table Sxx).

*Stachys* common garden

Of the 112 plants originally transplanted in 2016, 108 survived through the first year, and 103 survived through the second year. Plants had significantly higher biomass in 2016 when they received supplemental water (t = 12.094, p < 0.001). Overall, island genotypes grew modestly larger than their mainland relatives (t = 3.303, p = 0.067); the absolute difference in biomass across years was identical, with island plants supporting an average of 54.9 g of additional biomass in each year.

Consistent with observations from *Stachys* growing in situ, island and mainland genotypes sampled from the common garden had markedly different chemical compositions, both in terms of absolute abundance and the presence/absence of compounds (Figure 4b). The most pronounced differences between island and mainland genotypes were for mono- and sesquiterpenes, with island genotypes showing an approximate 100-fold reduction in the abundance of these compounds (Figure 4c). Mainland genotypes were generally consistent across populations in both the abundance and relative composition of leaf secondary compounds (Figure Sxx), and Santa Cruz Island genotypes did not differ based on whether they were grown on Santa Cruz Island versus the mainland (Figure Sxxx).

**Discussion**

Results vary based on traits measured as well as species

Overall effect of island/mainland differentiation was not significant for any traits, although went in the expected direction. However, these analyses were limited by the number of species pairs used in analysis. For example, even though spinescence clearly differed within Prunus and Heteromeles from island and mainland locations, the overall model of island/mainland differentiation was not significant because there were only two independent species-level contrasts, meaning that the d.f. for IM was only ~1.

Species-level differences perhaps more instructive, and here there was stronger evidence for island/mainland differentiation. Ideal approach would involve characterizing the degree of genetic differentiation for island and mainland genotypes: some species pairs (e.g. Heteromeles) are probably not very distinct based on mode of dispersal.

Spinescence heteroblasty recapitulates previous results

Cyanogenic glycoside results are novel and are consistent with reductions associated with loss of herbivores.

For common garden data, most contrasts were slightly less pronounced, although always in the same direction as traits from in situ plants.

For Stachys, results were much more clear and very obviously support strong differences between island and mainland genotypes. Here again, greater sampling from more species, as well as genetic data, would strengthen these results.

Stachys results generally consistent with the idea of a growth/defense tradeoff. Island plants are larger, more upright, woodier, and have lower levels of putative chemical defenses. However, terpenes are likely multifunctional and may be involved in UV resistance as well.

Island plants grew larger than their mainland relatives. While this result might seem counterintuitive, our common garden was set up to minimize the influence of gophers and deer. Had plants been exposed to these herbivores, biomass differences between island and mainland plants may have been different.

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