

NOT ALL PLANT TAXA DISPLAY TYPICAL LATITUDE-PROPAGULE SIZE GRADIENTS: A CASE STUDY IN *ARCTOSTAPHYLOS* L. (ERICACEAE)

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ABSTRACT

Proposed causes of the latitudinal-propagule size gradient invoke differences among biome structures or seed dispersal syndromes. Latitudinal seed-size gradients so far have been predominantly investigated using entire floras, prompting the question of whether such trends exist at smaller scales. Here we consider effects of latitude and elevation on fruit size between and within species in *Arctostaphylos* L. (Ericaceae), a zoochorous, primarily Californian chaparral shrub genus. We measured fruit size, strongly correlated with seed size in *Arctostaphylos*, in three species of this genus from multiple localities in the Sierra Nevada foothills, and conducted a character analysis of fruit size across the genus using the standard California flora plant manual (Baldwin et al. 2012). Across the genus we found a weak negative correlation between fruit size and latitude (0.0026 mm diameter/km) and a weak positive correlation between fruit size and elevation (1.3 mm diameter/km). AIC indicates that these trends are not explained by autocorrelation between fruit size and other variables such as maximum plant size. By contrast, intraspecific field data revealed a positive relationship between fruit size and both elevation and latitude. Propagule size gradients within *Arctostaphylos* oppose those reported for angiosperms globally. This contrast may result from uniformity of fruit structure and animal dispersal, disturbance ecology of chaparral, or local precipitation gradients characteristic of Mediterranean-type climates. Studies of propagule size gradients within taxa can uncover ecological mechanisms behind this trend that remain obscure at global scales.

Key Words: *Arctostaphylos*, California, elevation, fruit size, latitude, propagule size, Sierra Nevada foothills.

Variation in seed size influences a large number of ecological and physiological processes in plants (Kitajima and Myers 2008, Moles and Leishman 2008), such as trade-offs between seed mass and seed number or seedling survival. Seed size simultaneously may reflect multiple selective processes acting on the life history of plants. Here we examine patterns found within *Arctostaphylos* L. (Ericaceae; manzanita), which has a large number of species that vary greatly in fruit size. Fruits in this genus can contain 2–10 seeds that are variously and sometimes strongly fused into a group, which at maturity are surrounded by a mealy mesocarp and a thin exocarp. Generally, *Arctostaphylos* fruit are the dispersal propagule, dispersing seeds within as a single unit. Because seed and fruit mass are strongly correlated ($P = 0.01$, $\rho = 0.70$; Moore 2014, Parker 2015), here we use fruit size as a surrogate for seed size.

Global geographic trends in the distribution of ecological traits, such as the latitudinal seed size gradient in plants (e.g., Moles et al. 2007), compile together multiple evolutionary and ecological rela-

tionships within individual taxa that occur over smaller spatial and ecological scales. By restricting our study to the genus *Arctostaphylos*, we consequently hold a number of aspects constant that have been used to explain global patterns, such as variation in light environments, dispersal vectors, growth form, and vegetation type. We hope that these local patterns provide insight into significant trait variation seen within genera that have radiated into a variety of soil and climate conditions. By examining latitudinal and related gradients in fruit size in *Arctostaphylos*, we also can address questions of whether and how the global gradient represents a model for genera restricted to regions along that gradient or whether the global trends are scale-dependent. Does fruit size in all genera respond equally to the pressures of latitude and elevation?

Several hypotheses propose to explain latitudinal gradients in seed size (Moles et al. 2007). In our study, we test the following two: (1) Growth form correlates with seed size with woody plants having larger seeds than herbs (Lord et al. 1997, Wright et

al. 2007); tropical ecosystems contain a higher percentage of trees that typically have large seeds. (2) Vertebrate dispersal of fruits is considered to be more available in the tropics than the temperate zone, thereby freeing propagules from the size constraints necessary for effective wind dispersal (Wilson et al. 1989, Lord et al. 1997). In the context of *Arctostaphylos*, the genus varies considerably in overall plant size, which enables the hypothesis that larger plants have larger propagules (#1 above) to be tested directly. Furthermore, all species of *Arctostaphylos* are woody and benefit from animal-mediated dispersal. Therefore, if latitudinal propagule-size gradients can be attributed to differential frequency of dispersal mechanism (#2 above), then there should be no latitudinal gradient in *Arctostaphylos*.

In addition to the above two hypotheses, two more have been proposed that we do not here examine (Moles et al. 2007): (3) Seedlings in closed-canopy tropical forests require extra leaf surface to collect sufficient light in a shaded understory (Salisbury 1942). Finally, (4) lower latitude climates are more favorable to growth, including longer growing seasons and higher net primary productivity, which may also enable the growth of larger seeds. Climate and vegetational profiles of the California Floristic Province do not follow the global latitudinal gradients in either canopy closure or net primary productivity, due to the fact that the southern parts of California are drier, if warmer, than the northern parts, and the moisture profile also is tightly associated with elevation. *Arctostaphylos* is often associated with trees in habitats where it is found, but in most cases these trees do not form a closed canopy. As a consequence, testing either of the hypotheses that canopy closure or net primary productivity is outside of the scope of what can be confidently done using this genus.

Our working hypothesis is that fruit size variation in *Arctostaphylos* should match global patterns. Holding dispersal agents constant tests whether environmental gradients found within the California Floristic Province have an impact different from dispersal processes. Studies of seed size as a function of latitude over small spatial scales have supported global patterns, using as a model both the regional California flora (Baker 1972) or elsewhere (Mazer 1989). However, because the moisture gradient in California runs from south (arid) to north (mesic), contrary to global trends, we might as an alternative hypothesis anticipate a canopy-closure or drought-induced primary productivity gradient running from south to north as well. A positive elevational gradient in rainfall also exists in California, but Baker found that seed size at the floristic scale decreases with increasing elevation. If fruit size in *Arctostaphylos* runs contrary to the trends found by Baker for the California flora as a whole, then some aspect of the ecology of the genus is different from the processes responsible for the global propagule-size gradient.

We make similar predictions about the distance of a species from the coast, as more inland environments in California are drier and have more extreme temperatures. Because the coastline in California is largely north-south, longitude provides a rough estimate of coastal difference and continental climate for individual field samples.

Patterns in fruit size variation within *Arctostaphylos* should help evaluate alternative hypotheses concerning underlying influences in fruit-size geographic gradients. Disagreement in patterns between *Arctostaphylos* and in the global flora would imply that global-scale patterns are driven by characters that are invariant within *Arctostaphylos*, such as animal-dispersal or fire-stimulated persistent seed. Alternatively, a pattern consistent with the global pattern would suggest that ecological or evolutionary characteristics that vary among species drive the gradient. A lack of statistical pattern might suggest fruit variation within *Arctostaphylos* would be of stochastic or phylogenetic origin. *Arctostaphylos* species are thought to be chiefly dispersed by scatter-hoarding rodents, although other animals, including bears are known to disperse *Arctostaphylos* seeds (Parker 2015, Moore and Vander Wall 2015).

METHODS

Literature Floral Survey and Meta-Analysis of *Arctostaphylos*

There were two phases of data collection and analysis in this study. Because all species of *Arctostaphylos* are found naturally in California, we first used Baldwin et al. (2012) to compile a database of fruit size, elevation range, and regeneration strategy (whether species are able to resprout from burls) for all taxa ($n = 95$) in the genus. Baldwin et al. do not give latitudinal limits for any species, but geographic distributions are described in narrative form. Latitudes were inferred by matching the narrative descriptions in Baldwin et al. to geographic maps and software, primarily Google Earth (earth.google.com, accessed on 1 November 2008).

For each species, thirteen continuous variables were collected: minimum, median, and maximum values for fruit size, latitudinal range, altitudinal range, and distance from coast, plus maximum height at maturity. We chose to include both minimum and maximum values for the aforementioned variables because each may represent different endpoints in the factors influencing propagule size. For example, a species with a large latitudinal range might have large fruits at the southern limit of its range, but small fruits at the northern edge, which would not be recovered using a single latitude or fruit size variable. Baldwin et al. (2012) provides only qualitative information on the sizes of burls, so taxa were scored for presence (1) or absence (0) of burls. Taxa that sometimes have burls were scored as having burls for the purpose of this study. Taxa within

Arctostaphylos were resolved to the finest scale resolution possible; if a species was divided into subspecies as per Baldwin et al. (2012), then subspecies were used as data points. While this may introduce bias of phylogenetic non-independence of data, the amorphous distinction between biological species for much of the genus (Boykin et al. 2005) precludes useful phylogenetic controls for this analysis. Fruit volume was calculated from diameter under the assumption of a spherical fruit, which is generally a good assumption for *Arctostaphylos*. For those species with ellipsoid fruit, volume was calculated based on fruit dimensions assuming an oblate spheroid geometry.

Intraspecific Field Sampling

Fruits from three species of *Arctostaphylos*, *A. manzanita* Parry (common manzanita), *A. patula* Greene (greenleaf manzanita), and *A. viscida* Greene (whiteleaf manzanita) were collected in the western Sierra Nevada during the summer and early fall of 2008. Taxa were chosen for their wide geographic and elevational ranges, allowing for a meaningful comparison of fruit size and environmental variables, and for the accessibility of obtaining fruits. Fruit physical dimensions were measured and collection location recorded using GPS (latitude, longitude, elevation). Five fruits were collected and measured from each of the 330 plants sampled. Fruits collected from each plant were those that appeared healthy and well-developed, comparable in size to dropped fruit from previous seasons and not underdeveloped relative to other fruits on the plant. This choice might result in a bias toward larger fruit sizes; however, this should not affect trends within species because such biases would be systematic across study sites. The study area included accessible portions of chaparral communities, from the southern range of the study area northward, along California highways from 37°48' to 40°30' latitude and from 170 to 2500 m elevation.

Data Analysis

For each fruit size variable (minimum, maximum), we constructed generalized linear models using the generalized linear model (glm) function in R (R Core Development Team 2016) for each of the eight explanatory variables (height, burl presence/absence, max., min. and range of elevation, and max., min., and range of latitude). In addition to analyzing each explanatory variable individually against fruit size, we also analyzed each pair of explanatory variables against fruit size, as well the following blocks of variables: plant height with all elevation variables, plant height with all latitude variables, all elevation variables with all latitude variables, burl presence/absence with all elevation variables, and burl presence/absence with all latitude variables, and finally all eight variables together in one model. In

all models examining more than one explanatory variable, we also examined all relevant two-way interactions, but did not examine interactions more complex than two-way. We then used Akaike's Information Criterion (AIC) within R to select the best among the models that we tested.

In the intraspecific study, mean geometric fruit volume at maximum size of development was calculated for each plant sampled for the three (*A. manzanita*, *A. patula*, and *A. viscida*). For these species, we ran all combinations of linear models of fruit size as a function of latitude, longitude, and elevation, but without interaction terms between explanatory variables. As with the intraspecific data, we then used AIC to select the best model.

RESULTS

Interspecific Character Analysis

AIC analyses indicate that the best model explaining minimum fruit size includes both the height of the plant at maturity and also the distance that the species lives from the coast (Table 1, Fig. 1). Plant height is positively correlated with minimum fruit size. Relationships between minimum fruit size and coastal distance are remarkably flat, but are slightly positive for minimum distance from coast and slightly negative for maximum distance from coast. The null model in which minimum fruit size is unaffected by any of the variables under scrutiny is roughly a factor of 10⁶ worse than the best model using plant height and distance from coast.

The best model explaining median fruit size includes only median latitude, which correlates negatively with fruit size (Table 1, Fig. 2). However, this best model is not more than twenty times as likely as eight other models, including the null model. Most, but not all, of these other models do include latitude as a covariate, however.

The best model explaining maximum fruit size includes all of the explanatory variables that we measured (Table 1, Fig. 3). In this model, fruit size decreases with increasing latitude, and increases slightly with increasing elevation and with fruit size. Distance from the coast seems to correlate positively with maximum fruit size, but statistically this effect may be dominated by a few very wide-ranging species. The null model in which maximum fruit size is independent of both plant height and minimum latitude is roughly 10⁷ times worse.

Intraspecific Field Sampling

Summary statistics for our field samples are presented in Table 2. The best model explaining fruit size in *A. manzanita* includes elevation, latitude, and longitude (Table 3), which is more than 10⁴ times more likely than a null model. Regression on these variables reveals that fruit size increases with both

TABLE 1. AIC-based model selection results explaining fruit size in *Arctostaphylos* based on Baldwin et al. (2012). The best model (lowest AIC) score is shown for minimum, median, and maximum fruit size, as well as selected other models including the null model and all models at least 5% as likely as the best model, and the best runner-up model less than 5% as likely as the best model. “Inland” in models refers to the distance from each *Arctostaphylos* taxon to the nearest coast.

| Dependent variable | Model | AIC score | Akaike weight (relative likelihood) |
|--------------------|--|-----------|-------------------------------------|
| Min. fruit size | Plant height + min. inland + max. inland | 986.84 | 1 |
| | All parameters | 994.15 | 0.026 |
| | Null | 1015.86 | 5×10^{-7} |
| | | | |
| Med. fruit size | Med. latitude | -256.23 | 1 |
| | Med. latitude + med. inland | -253.68 | 0.28 |
| | Med. latitude + burl | -253.64 | 0.27 |
| | Burl | -253.39 | 0.24 |
| | Plant height + med. latitude | -253.33 | 0.24 |
| | Med. elevation + med. latitude | -252.44 | 0.15 |
| | Null | -252.24 | 0.14 |
| | Med. inland | -250.51 | 0.06 |
| | Plant height | -250.44 | 0.06 |
| | Med. elevation | -250.36 | 0.05 |
| | Plant height + burl | -249.86 | 0.04 |
| | | | |
| | | | |
| Max. Fruit size | All parameters | 955.23 | 1 |
| | Plant height + min. inland + max. inland | 959.47 | 0.12 |
| | Plant height + maximum latitude | 965.75 | 0.005 |
| | Null | 988.09 | 7.3×10^{-8} |
| | | | |

elevation (Fig. 4; Table 4) and latitude (Fig. 5; Table 4), and decreases moving eastward (Fig. 6; Table 4). The best model explaining fruit size in *A. viscida* includes both latitude and elevation; however, several other models have likelihoods at least 5% that of the best model, some involving longitude (Table 3). This model is over 100 times more likely than the null model. Using regression, fruit size in *A. viscida* increases with elevation (Fig. 4; Table 4) and with latitude (Fig. 5; Table 4). The regression line of best fit suggests that fruit size in *A. viscida* appears to decrease moving eastward (Fig. 6; Table 4) as in *A. manzanita*, but the effect is very small if it is real. The best model explaining fruit size in *A. patula* includes longitude and no other variables. However, all seven other models are at least 5% as likely as the best model, including the null model (Table 3). Regression lines of best fit suggest that fruit size in *A. patula* decreases with elevation (Fig. 4; Table 4), increases with latitude (Fig. 5; Table 4), and decreases moving eastward (Fig. 6; Table 4), if these relationships are real.

DISCUSSION

Initially, we set out to test two hypotheses regarding the latitudinal (and Baker’s elevational) propagule-size gradients. The hypothesis that larger plants tend to have larger propagules than smaller plants is largely borne out: plant height is correlated with both minimum and maximum fruit size in the best model, and the correlation is strongly positive. The hypothesis that a latitudinal gradient in dispersal mode is responsible for the latitudinal gradient in

propagule size does not agree with our data, because this hypothesis predicts that there should be no latitudinal gradient in the universally animal-dispersed *Arctostaphylos*. Despite this, median fruit size correlates negatively with latitude at an interspecific level in the genus, while at least *A. manzanita* and possibly *A. viscida* and *A. patula* as well see fruit size correlating positively with latitude. In all of these trends that we observed, the effect sizes are not large; most of the variation in fruit size is not determined by elevation, latitude, or any other variable that we investigated. However, because we are investigating a geographically small area relative to the global scale of the latitudinal seed size gradient, we should not expect the effect sizes to be large over this small scale. While *Arctostaphylos* displays the same fruit size trends with latitude at both the global (e.g., Moles et al. 2007) and floristic (Baker 1972) scale, these trends are not replicated on the intraspecific level in any of the three species tested, and *A. manzanita* and possibly *A. viscida* and *A. patula* as well exhibit the opposite trend. Furthermore, all measures of *Arctostaphylos* that show a statistically significant trend show a positive correlation between fruit size and elevation, in contrast to Baker’s (1972) findings for the California flora as a whole. We find the variation in the fruit size/latitude relationship between different taxonomic levels and between individual species somewhat surprising. We cannot tell from these data whether the differences in intraspecific trends result from these three species being anomalous, or if fruit size gradients typically change between species and as a function of taxonomic scale. *A. manzanita*, *A. viscida*, and *A. patula* are all widespread in Califor-

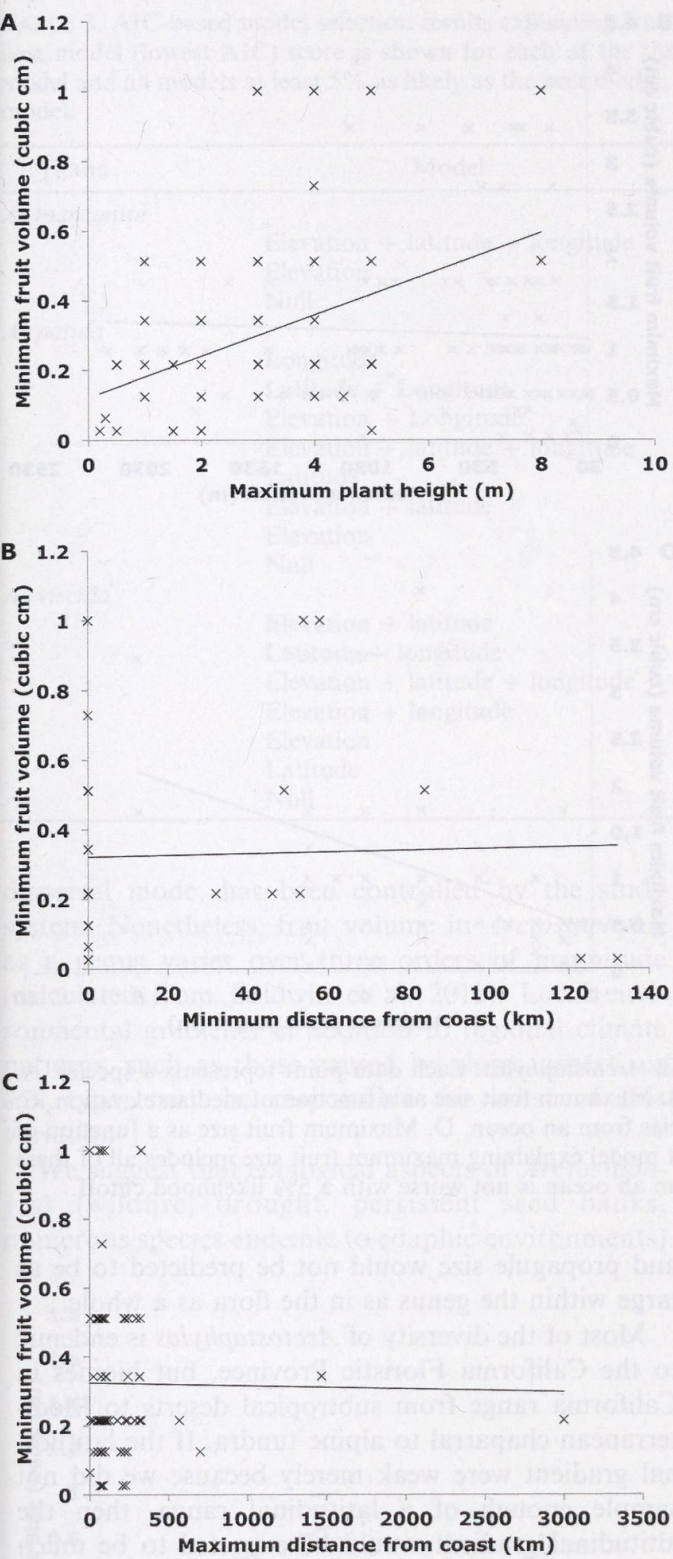


FIG. 1. Graphs of minimum fruit size (in cubic centimeters) in *Arctostaphylos*, based on data from Baldwin et al. (2012). Each data point represents a species. A. Minimum fruit size as a function of maximum plant height. B. Minimum fruit size as a function of the closet proximity of a species' range to the ocean. C. Minimum fruit size as a function of the greatest distance a species occurs from an ocean. AIC analysis (Table 1) indicates that all three of these explanatory variables together make for the best prediction of minimum fruit size.

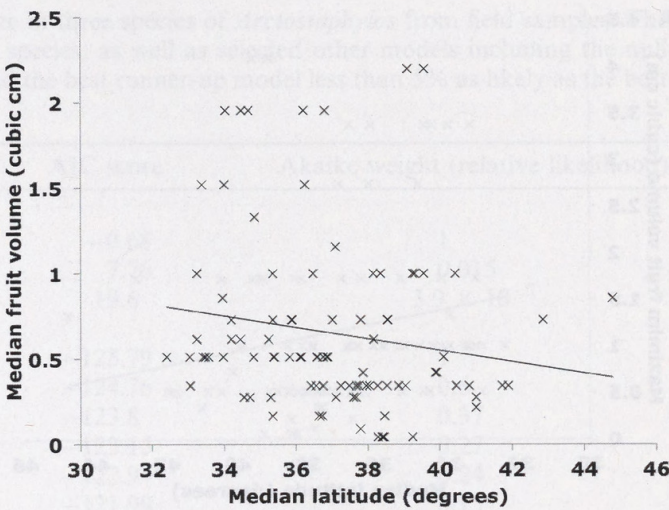


FIG. 2. Graph of median fruit size (in cubic centimeters) in *Arctostaphylos* as a function of median latitude at which a species occurs. Each data point represents a species. While AIC analysis (Table 1) suggests that the best model explaining median fruit size includes only latitude, several other models using other variables (including a null model) are not statistically worse by a 5% likelihood cutoff.

nia, in contrast to the local endemics ($n = 65/95$ from our character analysis) with restricted ranges composing the majority of species in the genus. Because most of the larger-seeded species with broad geographic ranges are found in southern California, examining intraspecific patterns in these species would test the consistency of the reversal of the correlation at the species scale.

Because the Mediterranean-climate of California becomes moister at higher latitude, the moisture pattern represents a localized reversal of the global aridity gradient from equator to pole. Further, a large number of species in *Arctostaphylos* are also local endemics that occur near the central and northern Pacific coast of California in moderate maritime climates. Thus, if fruit size in *Arctostaphylos* increases with moisture and not temperature, we would predict a positive relationship between fruit size and both latitude and elevation. At the interspecific level, maximum fruit size increases with elevation, which matches a moisture gradient. We recovered the same pattern in *A. manzanita* and possibly the other two species as well. In contrast to a global moisture correlation, Baker (1972), who examined seed mass (not fruit volume), found significant differences between seed mass in moist versus arid communities in the California flora. In his studies, seed mass increases in more arid communities. In all gradients that we examined, fruit size in *Arctostaphylos* either runs counter to the trends that Baker found or exhibits no significant trend, implying that the processes responsible for seed mass gradients in California as a whole do not determine what happens in *Arctostaphylos*.

Phylogeny is known to be relevant to propagule size but we did not control for it (Moles et al. 2005). The phylogeny of *Arctostaphylos* is currently unre-

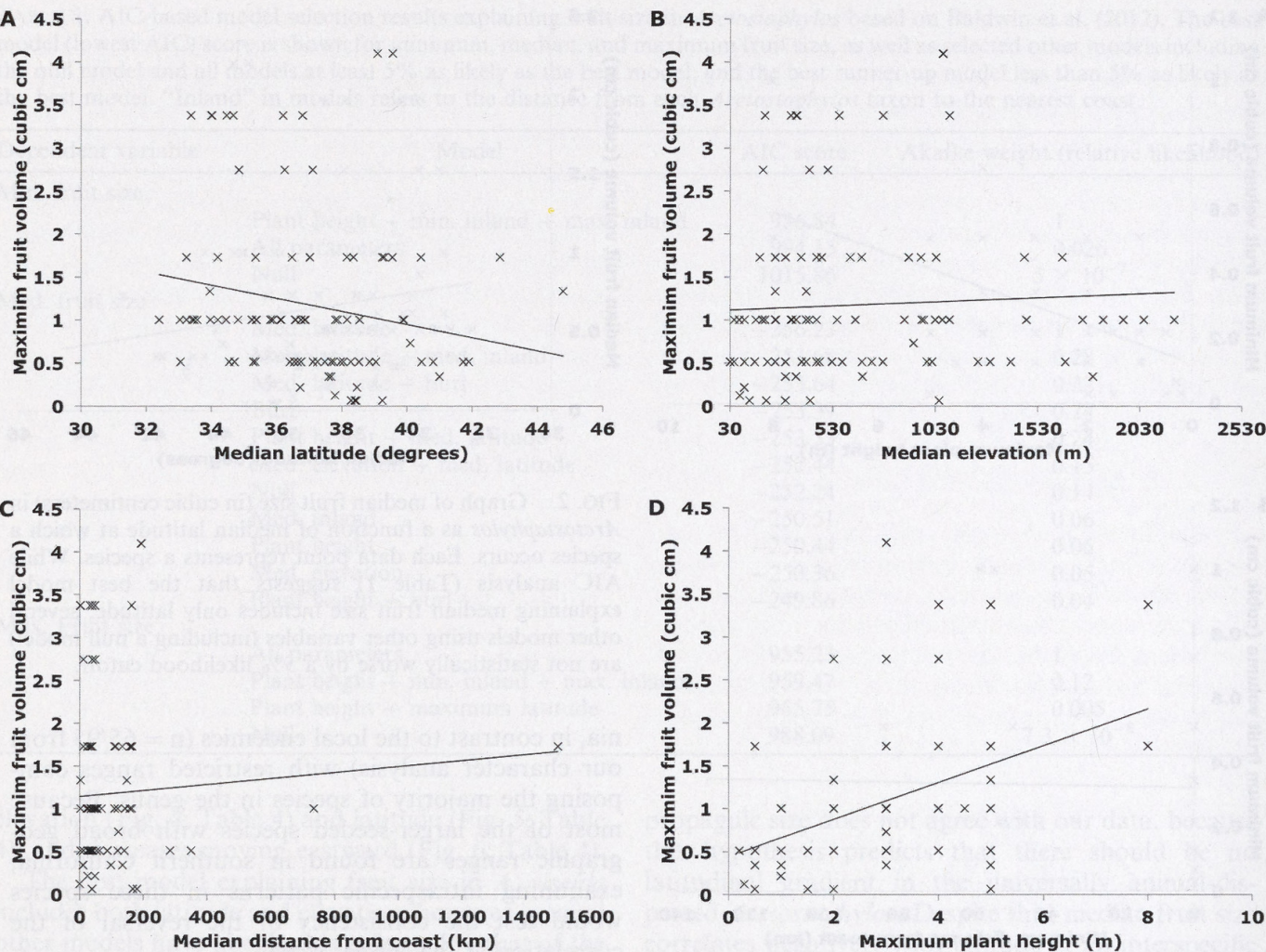


FIG. 3. Graphs of maximum fruit size (in cubic centimeters) in *Arctostaphylos*. Each data point represents a species. A. Maximum fruit size as a function of median range of latitude. B. Maximum fruit size as a function of median elevation. C. Maximum fruit size as a difference of median distance of a species from an ocean. D. Maximum fruit size as a function of plant height. AIC analysis (Table 1) suggests that while the best model explaining maximum fruit size includes all of these variables, a model including only plant height and distance from an ocean is not worse with a 5% likelihood cutoff.

solved, but appears to be divided into two large clades (Boykin et al. 2005, Wahlert et al. 2009); when the phylogeny is better resolved, controlling for it may account for some currently unexplained variation. Next, while individual species of *Arctostaphylos* possess characteristic sizes, almost all are shrubs ranging from 0.5 m to about 3.0 m in height. *Arctostaphylos uva-ursi* (L.) Spreng., for example, as an alpine or coastal species, is smaller, but its removal as an outlier does not affect the strength of correlations. As a consequence, the variation in height within a flora containing both trees and herbs will be greater than that contained solely within *Arctostaphylos*; thus, relationships between height

and propagule size would not be predicted to be as large within the genus as in the flora as a whole.

Most of the diversity of *Arctostaphylos* is endemic to the California Floristic Province, but biomes in California range from subtropical deserts to Mediterranean chaparral to alpine tundra. If the latitudinal gradient were weak merely because we did not sample enough of a latitudinal range, then the altitudinal gradient would be expected to be much stronger, which it is not. Selection for traits involved in fruit size gradients may therefore be weak in *Arctostaphylos*. One potential explanation for weak, nonexistent, or even reversed gradients is that the primary driver of the latitudinal gradient, namely

TABLE 2. Summary statistics of our intraspecific field study of *Arctostaphylos* fruit size as a function of geographic variables. Fruit size is in units of cubic centimeters. The abbreviation “SD” stands for standard deviation.

| Taxon | Fruit size mean | Fruit size SD | Elevation mean | Elevation SD | Latitude mean | Latitude SD |
|---------------------------------|-----------------|---------------|----------------|--------------|---------------|-------------|
| <i>Arctostaphylos manzanita</i> | 0.72 | 0.27 | 737 | 334 | 39.9 | 0.7 |
| <i>Arctostaphylos patula</i> | 0.55 | 0.13 | 1777 | 244 | 39 | 0.8 |
| <i>Arctostaphylos viscida</i> | 0.21 | 0.05 | 875 | 267 | 39 | 1 |

TABLE 3. AIC-based model selection results explaining fruit size in three species of *Arctostaphylos* from field samples. The best model (lowest AIC) score is shown for each of the three species, as well as selected other models including the null model and all models at least 5% as likely as the best model, and the best runner-up model less than 5% as likely as the best model.

| Taxon | Model | AIC score | Akaike weight (relative likelihood) |
|---------------------|----------------------------------|-----------|-------------------------------------|
| <i>A. manzanita</i> | Elevation + latitude + longitude | −0.68 | 1 |
| | Elevation | 7.76 | 0.015 |
| | Null | 19.6 | 3.9×10^{-5} |
| <i>A. patula</i> | Longitude | −125.79 | 1 |
| | Latitude + Longitude | −124.76 | 0.6 |
| | Elevation + Longitude | −123.8 | 0.37 |
| | Elevation + latitude + longitude | −123.15 | 0.27 |
| | Latitude | −122.94 | 0.24 |
| | Elevation + latitude | −121.99 | 0.15 |
| | Elevation | −121.4 | 0.11 |
| | Null | −120.8 | 0.083 |
| <i>A. viscida</i> | Elevation + latitude | −345.84 | 1 |
| | Latitude + longitude | −345.7 | 0.94 |
| | Elevation + latitude + longitude | −345.42 | 0.81 |
| | Elevation + longitude | −344.8 | 0.59 |
| | Elevation | −341.73 | 0.13 |
| | Latitude | −337.52 | 0.016 |
| | Null | −336.06 | 0.0075 |

dispersal mode, has been controlled by the study system. Nonetheless, fruit volume in *Arctostaphylos* as a genus varies over three orders of magnitude (calculated from Baldwin et al. 2012). Local environmental gradients in addition to regional climate patterns, such as those caused by slope, aspect, or soil type, may be responsible for most of this variation.

We suggest that ecological aspects of *Arctostaphylos* (wildfire, drought, persistent seed banks, numerous species endemic to edaphic environments)

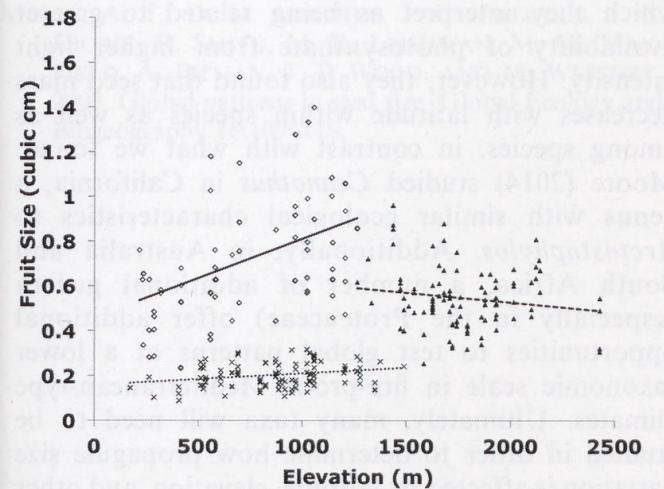


FIG. 4. Regressions of fruit size as a function of elevation in field samples of three species of *Arctostaphylos*. Open diamonds and solid lines represent *A. manzanita*, filled triangles and dashed lines *A. patula*, x symbols and dotted lines *A. viscida*. Summary statistics for these distributions are available in Table 2, and AIC analysis of statistical significance in Table 3.

may be driving the observed patterns. Species living in edaphic environments could be predicted to have less resources with which to make fruits, and so their fruits would be smaller. High-elevation environments in California are generally dominated by granitic soils, with the result that edaphic species at low elevation may account for the interspecific fruit size gradient in the genus. However, *A. manzanita* does not grow in edaphic environments, yet still increases fruit size with elevation, so edaphic environments alone cannot explain the elevational fruit size gradients in *Arctostaphylos* at all levels. *Arctostaphylos* differs from most other plant genera in its response to wildfire. In the Sierra Nevada, *Arctostaphylos patula* resprouts following fire from burls, as do some *A. manzanita* (only subsp. *roofter* [Gankin] P. V. Wells), but not *A. viscida* (Baldwin et al. 2012). Yet, all species of *Arctostaphylos* live in fire-prone areas, and all establish new individuals from persistent seed banks in a high-light, droughty, post-fire environment. Variation in fruit size (and seed size) may reflect the geographic climate variation as it influences the difficulty in establishing seedlings in the post-fire environment. Drought should select for larger fruit (seeds) so that seedlings have a better opportunity to establish root systems deep enough to survive a more severe summer drought. While elevation relaxes the moisture deficit, growing season length is reduced and large fruit size may be favored by selection to provide seedlings more of chance to establish prior to winter storms and burial in snow. Because rodents are found throughout the elevational gradient of *Arctostaphylos* and because they are the chief

TABLE 4. Linear regression coefficients for relationships between fruit size and latitude, elevation, and longitude for *Arctostaphylos manzanita*, *A. patula*, and *A. viscida*. Statistical significance of these relationships addressed via AIC-based model selection, the results of which are presented in Table 3.

| Taxon | Explanatory variable | Slope | R ² |
|---------------------|----------------------|--------------------------------|----------------|
| <i>A. manzanita</i> | Elevation | 0.4 cm ³ /km | 0.18 |
| | Latitude | 0.84 cm ³ /degree | 0.045 |
| | Longitude | 0.13 cm ³ /degree | 0.13 |
| <i>A. patula</i> | Elevation | −0.09 cm ³ /km | 0.025 |
| | Latitude | 0.036 cm ³ /degree | 0.041 |
| | Longitude | 0.055 cm ³ /degree | 0.055 |
| <i>A. viscida</i> | Elevation | 0.05 cm ³ /km | 0.068 |
| | Latitude | 0.0097 cm ³ /degree | 0.034 |
| | Longitude | 0.0089 cm ³ /degree | 0.0089 |

dispersal agents, differences in dispersal ecology are unlikely to be responsible for the gradients in fruit size that we observed. As such, one might predict that there would be an elevation at which a maximum fruit size is attained, as supported by *A. manzanita* being below this maximum, but *A. viscida* and *A. patula* straddling or above it. If so, then similar patterns with elevation could be obtained from southern California inland manzanitas. Moore (2014) addressed in similar questions in other species of *Arctostaphylos* and *Ceanothus* L. and found that *Arctostaphylos* does not conform to global patterns of fruit and seed size, with which our results agree.

We are aware of few studies that have examined propagules at a scale smaller than the flora most

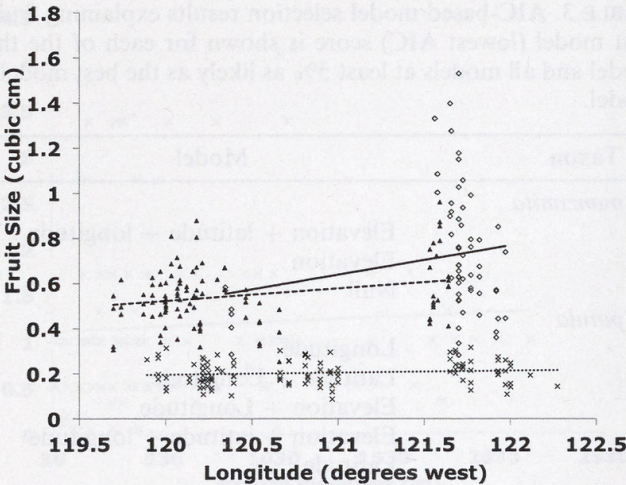


FIG. 6. Regressions of fruit size as a function of longitude in field samples of three species of *Arctostaphylos*. Open diamonds and solid lines represent *A. manzanita*, filled triangles and dashed lines *A. patula*, x symbols and dotted lines *A. viscida*. Summary statistics for these distributions are available in Table 2, and AIC analysis of statistical significance in Table 3.

have been meta-analyses using published range sizes. Investigating fruit size patterns at taxonomic scales lower than global or regional floras indicates that while patterns may match or contrast with global patterns, underlying mechanisms are likely to be driven by ecological issues specific to the taxon. In this study we tried to hold constant a number of ecological or evolutionary processes thought to drive the global pattern. Our results indicate that *Arctostaphylos* does not consistently abide by the same patterns as the global flora. Murray et al. (2003, 2004) investigated seed size in Australian *Glycine* L. (Fabaceae), and found similar results to ours in *Arctostaphylos*: seed mass increases with decreasing latitude and with increasing aridity, which they interpret as being related to greater availability of photosynthate from higher light intensity. However, they also found that seed mass decreases with latitude within species as well as among species, in contrast with what we found. Moore (2014) studied *Ceanothus* in California, a genus with similar ecological characteristics to *Arctostaphylos*. Additionally, in Australia and South Africa, a number of additional genera (especially in the Proteaceae) offer additional opportunities to test global patterns at a lower taxonomic scale in fire-prone Mediterranean-type climates. Ultimately, many taxa will need to be studied in order to determine how propagule size variation is affected by latitude, elevation, and other macroecological variables.

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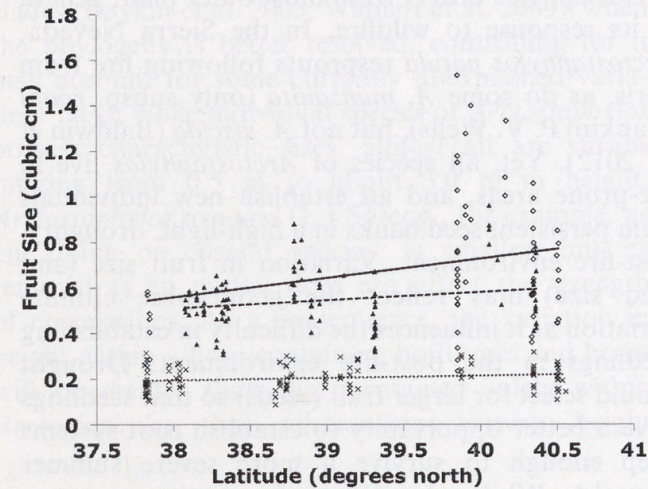


FIG. 5. Regressions of fruit size as a function of latitude in field samples of three species of *Arctostaphylos*. Open diamonds and solid lines represent *A. manzanita*, filled triangles and dashed lines *A. patula*, x symbols and dotted lines *A. viscida*. Summary statistics for these distributions are available in Table 2, and AIC analysis of statistical significance in Table 3.

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