

Fine-scale spatial patterns of density and fitness in two flowering plant populations in the Upper
Great Lakes Region

BIOS 569: Practicum in Field Biology

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Abstract

Patterns of fitness and spatial distribution within plant populations may reflect patterns that occur on the species range level. The abundant center hypothesis predicts that individuals at the center of a species' range will be more abundant and produce more offspring. This study examined whether these range-level patterns occurred on the population level for two flowering plant species: *Barbarea vulgaris* (hermaphroditic) and *Silene latifolia* (dioecious), specifically testing whether (1) density and fitness decreased away from the center of the population, whether (2) fitness increased with density, and within the dioecious population, whether (3) females were more centrally located and if (4) female fitness correlated with nearest male neighbor distance. For each population, I identified all individuals, mapped their location, and estimated their fitness. Additionally, I calculated distance from the center of the population and distance to the nearest neighbor for every individual. Results for *B. vulgaris* showed that density and fitness were actually greater at the periphery of the population, and that height increased with density. For *S. latifolia*, there was no conclusive pattern in spatial distribution, but there was a negative relationship between density and fitness, suggesting that intraspecific competition may play a major role in *S. latifolia* life history. Furthermore, male fitness was shown to decrease when female neighbors were closer, suggesting strong intersexual competition and a competitive advantage on the part of females. Overall, the abundant center distribution did not occur on the population level, though several other interesting trends did arise.

Introduction

Within populations of flowering plants, density and fitness can vary greatly over space and time. These factors can be controlled by several factors, including species-species

interactions such as herbivory and pollination, reproductive morphology, and the availability of nutrients, sunlight, and water (Maron & Crone, 2006; Kunin, 1993; Freeman *et al.*, 1976; Kluth & Bruelheide, 2005). Understanding the fine-scale structure of plant populations, specifically whether density and fitness are randomly distributed or exhibit patterns, is critical to understanding their interactions with the rest of the community.

Predictions about structure within a population can potentially be made based on that within the entire species' range. Patterns of distribution and fitness on the species range level are well-documented and often described by the abundant center hypothesis (ACH), which predicts that a species' greatest abundance occurs at the center of its geographic range and decreases toward the periphery (Henvegald & Haeck, 1982; Brown & Mehlman, 1995). One commonly accepted explanation of this pattern is that a species' abundance is coupled with environmental gradients such that abundance is greatest at the optimal point along the gradient and decreases with distance away from that point, as shown by Van Couwenberghe *et al.* (2013) for 243 vascular species.

The ACH also describes patterns in fitness, predicting that individuals in central populations will produce more offspring than those in peripheral populations, again following from the idea that environmental conditions will be more favorable at the center, which will in turn produce more fit individuals (Samis & Eckert, 2007). Indeed, even though many studies have failed to support the ACH for patterns of abundance (Sagarin & Gaines, 2002), several have shown central populations to contain more fit individuals than peripheral populations, despite abundance being uniform throughout the range. Herlihy and Eckert (2005) found that individuals in peripheral populations of Canadian columbine (*Aquilegia canadensis*) produced fewer inflorescences and smaller flowers than those at the center, despite populations being the same

size and density. This shows that patterns in fitness may exist independently of patterns in abundance.

It follows that these patterns of abundance and fitness may also occur on the population level, with individuals occurring most densely at a point of optimal environmental conditions and decreasing in density away from that point. Individuals at the center of a population are more likely to experience successful pollination, which in turn allows them to also produce more offspring (Kunin, 1993), which could also contribute to a dense-center distribution. Pollinator visitation decreases with decreasing density (Kunin, 1997), meaning that individuals toward the periphery may be more pollen limited and therefore less fit.

Sexual morphology may also play an important role in spatial patterns of density and fitness within a population. While the majority of flowering plants are hermaphroditic, about 6% of angiosperm species are dioecious (Renner and Ricklefs, 1995), which means that populations contain both male and female plants. Freeman *et al.* (1976) found that among dioecious species, males were consistently less sensitive to water stress than females, and that females required a more favorable, moist soil to support seed production. This suggests that sex ratio can vary significantly with environmental gradients. In particular, females may tend to be located in high-quality areas of the population, while males may be more widely distributed. If high quality habitat coincides with the central portion of the population, as predicted by ACH, then females may be more likely to occur in these regions. Wang *et al.* (2013) found that for the dioecious tree, *Rhamnus davurica*, female fruit set increased as distance to the nearest male decreased, concluding that pollen limitation was a key determining factor for female fitness. It follows from this that the distance between male and female individuals may affect fitness within dioecious

flowering plant populations, namely, that female fitness will increase with decreasing distance to the nearest male conspecific.

The goal of this study was to analyze the spatial distribution of fitness and density within flowering plant populations, using range-level patterns to predict population-level patterns. Two populations were observed: *Barbarea vulgaris* R. Br. (Barassicaceae) and *Silene latifolia* Poir. (Caryophyllaceae). *B. vulgaris* is a hermaphroditic biennial with passive seed dispersal, though seeds can also be dispersed by animals given their adhesive mucus (Rutledge *et al.*, 1996). *B. vulgaris* can reproduce both sexually – pollinated by flies and bees – and asexually, with buds arising from roots, and is also self-compatible (Tachibana *et al.*, 2010). *S. latifolia* is a dioecious annual, which also disperses seeds passively. *S. latifolia* reproduces sexually and has moth pollinators (Barluenga *et al.*, 2011).

For each species, I estimated the fitness and mapped the location of every individual in order to assess patterns in geographic distribution. I hypothesized that both (1) population density and fitness decrease away from the center of the population, while (2) fitness increases with population density. Additionally, for *S. latifolia*, I hypothesized that (3) females are more abundant at the center of a population and (4) their fitness increases as distance to the nearest male decreases.

Methods

Study organisms

B. vulgaris is an erect, slightly branched herb, usually 2-3 feet high with racemes of yellow, 4-parted, ½” wide flowers. Flowering occurs from April to June. *B. vulgaris* does not have specific substrate requirements, and can tolerate a variety of soil compositions and moisture

levels (Baillargeon *et al.*, 2009). *S. latifolia* is an erect herb, usually 1-3 feet tall, with clusters of flowers growing on a multi-branched inflorescence. Flowers have a tubular, inflated calyx (larger in females than males) and five white, deeply lobed petals. Flowering occurs from June to October, and plants can grow in a variety of soil conditions but do not tolerate shade (Barkley *et al.*, 2005).

Study Site and Data collection

Studies were conducted at the University of Notre Dame Environmental Research Center in the Upper Peninsula of Michigan between June and July of 2014. Populations were observed in a field (46°14'42.8"N 89°33'04.8"W) bounded on one side by marsh and on the remaining sides by northern hardwood forest.

For each population (N=2), I identified every individual (*B. vulgaris* = 196, *S. latifolia* = 704). I estimated fitness for each individual in two ways: plant height (distance from ground to tallest point on plant) and flower number (including buds and cut stems).

In order to record the location of individuals, I set up two perpendicular meter tapes to represent a coordinate plane, with one transect representing the x-axis and the other the y-axis. An individual's relative position was determined by running a measuring tape from the base of the stem of the plant to the main grid.

The center of the population was identified as the average of the two most extreme x and y values for each species. A small group of individuals in each species (see Figure 1) were not included in the calculation of the center of the population due to the fact that they were isolated from the rest of the population by a considerable distance. For every individual, distance away from the center was calculated, as was distance to the nearest neighbor, which was used as a

proxy for density as per Clark & Evans (1954). For *S. latifolia*, I calculated both distance to nearest male and distance to nearest female plant for every individual.

Statistics

For each population, I divided the range of x-values into five equal parts and the y-values into three in order to create a grid (See Figure 1). The three central blocks in the grid were designated as “central,” and the remaining as “peripheral.” Height and flower number were also converted to categorical values by taking the mean and designating those greater than the mean as “tall” and “many-flowered,” respectively, and those below the mean as “short” and “few-flowered,” respectively. Nearest neighbor data was also converted to categorical values, again by taking the mean, and designating those individuals with a nearest neighbor farther than the mean value as having a “far” nearest neighbor, and those with a nearest neighbor as than the mean value as having a “close” nearest neighbor.

None of the recorded variables had a normal distribution, so Mann-Whitney U tests were used instead of t-tests in order to compare fitness and density in the central and peripheral parts of the populations. Linear regressions were used to compare distance from the center of the population to flower number, height, and nearest neighbor data. The latter three variables were transformed to their natural log in order to achieve a symmetrically distributed plot of residuals versus predicted values. Additionally, chi-square tests were used to compare the ratio of few flowered and many flowered plants, short and tall plants, and individuals with close and far nearest neighbors between the central and peripheral groups. All statistical analyses were performed using SYSTAT Version 13.

Results

Patterns of Spatial Distribution

The *B. vulgaris* population consisted of 196 individuals: 70 central and 126 peripheral (Fig. 1a). The distance between individuals and their nearest neighbor was significantly larger among central individuals (mean = 0.999 ± 0.142 m) than peripheral individuals (mean = 0.789 ± 0.155 m; Mann-Whitney U test, $U = 5,730$, $df = 1$, $p = 0.0005$), suggesting that population density was greater among peripheral individuals. There was not a significant relationship between nearest neighbor distance and distance from center, though the p value did approach significance ($R^2 = 0.0176$, $df = 194$, $p = 0.064$). The relative frequency of individuals with a close nearest neighbor was significantly higher in the peripheral portion of the population ($\chi^2 = 11.47$, $df = 1$, $p = 0.0007$) (see Table 1a), again suggesting that population density was higher in the peripheral portion of the population.

The *S. latifolia* population consisted of 704 individuals, with 124 located centrally and 580 located peripherally (Fig. 1b). Consistent with *B. vulgaris*, the distance to the nearest neighbor was significantly larger among central individuals (0.724 ± 0.111 m) compared to peripheral individuals (0.383 ± 0.035 m; Mann Whitney U test, $U = 41,689$, $df = 1$, $p = 0.005$). There was no relationship between nearest neighbor distance and distance from center ($R^2 = 0.0012$, $df = 702$, $p = 0.359$). The relative frequency of individuals with a close nearest neighbor did not differ between the central and peripheral portions of the population ($\chi^2 = 2.69$, $df = 1$, $p = 0.101$) (see Table 1b).

Patterns of Fitness Distribution

Measures of fitness varied substantially for individuals of *B. vulgaris*. Flower number ranged from 11 to 766 (mean = 79.89 ± 5.58), and plant height ranged from 8.1 to 63.6 cm (mean = 31.15 ± 0.72). There was a significant positive relationship between flower number and distance from center ($R^2 = 0.048$, $df = 194$, $p = 0.002$) as well as height and distance from center ($R^2 = 0.122$, $df = 194$, $p < 0.0001$) (see Figure 2). There was no significant relationship between distance to nearest neighbor and flower number ($R^2 = 0.019$, $df = 1$, $p = 0.054$), but height increased as distance to nearest neighbor decreased ($R^2 = 0.048$, $df = 1$, $p = 0.002$), suggesting that individuals were taller where population density was greater.

Central individuals had an average flower number of 69.629 ± 4.843 and an average height of 29.276 ± 1.118 cm, while peripheral individuals had an average flower number of 85.595 ± 8.231 and average height of 32.196 ± 0.920 cm, but neither flower number nor height were significantly different between central and peripheral individuals (Mann-Whitney U test, $U = 4,109$, $df=1$, $p = 0.43$; $U = 3,774$, $df = 1$, $p = 0.095$). The relative frequency of many-flowered plants did not differ significantly between central and peripheral portions of the population ($\chi^2 = 1.08$, $df = 1$, $p = 0.298$;) (see Table 2a), nor did it differ between those with near or far neighbor ($\chi^2 = 3.328$, $df = 1$, $p = 0.068$) (see Table 1b). However, the relative frequency of short plants was higher in the central portion of the population ($\chi^2 = 6.27$, $df = 1$, $p = 0.012$) (see Table 3a) and among individuals with a far nearest neighbor ($\chi^2 = 13.277$, $df = 1$, $p = 0.0002$) (see Table 3b), suggesting that plants were shorter in the center of the population and where population density was low.

Fitness also varied greatly for *S. latifolia*. Flower number ranged from 0 to 66 (mean = 6.88 ± 0.25), and plant height ranged from 4.8 to 128.9 cm (mean = 50.51 ± 0.60). There was not

a significant relationship between flower number and distance from center ($R^2 = 0.0003$, $df = 702$, $p = 0.624$) or between height and distance from center ($R^2 = 0.005$, $df = 702$, $p = 0.0519$) (see Figure 3). There was, however, a significant positive relationship between flower number and nearest neighbor distance ($R^2 = 0.006$, $df = 702$, $p = 0.039$) and height and nearest neighbor distance ($R^2 = 0.018$, $df = 702$, $p = 0.0004$), suggesting that individuals were more fit in areas of low population density.

Central individuals in the *S. latifolia* population had an average flower number of 6.919 ± 0.642 and an average height of 48.105 ± 1.411 cm. Peripheral individuals had an average flower number of 6.874 ± 0.276 and an average height of 51.02 ± 0.660 cm. Plants were significantly smaller in the central portion of the population (Mann-Whitney U test, $U = 31$, 771.5 , $df = 1$, $p = 0.041$), but flower number did not significantly vary (Mann-Whitney U test, $U = 32,626$, $df = 1$, $p = 0.103$). When plants were assessed categorically for fitness, the relative frequency of plants with many flowers did not vary among central and peripheral areas ($\chi^2 = 3.565$, $df = 1$, $p = 0.059$) (see Table 4a), nor did it differ significantly between individuals with close or far nearest neighbors ($\chi^2 = 0.426$, $df = 1$, $p = 0.514$) (see Table 4b). The relative frequency of tall plants did not vary between the center and the periphery ($\chi^2 = 0.0017$, $df = 1$, $p = 0.967$) (see Table 5a), but the relative frequency of short plants was higher among individuals with close neighbors ($\chi^2 = 3.894$, $df = 1$, $p = 0.048$) (see Table 5b), or where density was greater.

Patterns of Sexual Distribution

Of the 704 *S. latifolia* individuals, 67.2% were female and 32.8% were male. There were significantly more females than males ($\chi^2 = 83.188$, $df = 1$, $p \ll 0.0001$). The relative frequency of females and males, however, did not differ significantly between central and peripheral

portions of the population ($\chi^2=0.021$, $df=1$, $p = 0.88$). Among females, neither height nor flower number was correlated with distance to the nearest male individual ($R^2 = 0.0002$, $df = 471$, $p = 0.75$; $R^2 = 0.0059$, $df = 1$, $p = 0.095$), but flower number did increase with distance way from the center of the population ($R^2 = 0.010$, $df = 471$, $p = 0.027$). Among males, both flower number and height were positively correlated with distance to the nearest female ($R^2 = 0.043$, $df = 229$, $p = 0.001$; $R^2 = 0.033$, $df = 229$, $p = 0.019$), suggesting that males tended to be taller and have more flowers when their nearest female neighbor was farther away.

Discussion

Using the patterns predicted by the ACH, I hypothesized that population density and fitness would decrease away from the center of the population, with nearest neighbor distance being used as a proxy for density. Within the population of *B. vulgaris*, density was higher in the periphery, and both flower number and height increased with distance away from the center of the population. These patterns were the exact opposite of what I predicted, and may suggest that optimal soil conditions occur at the edges of the field and deteriorate toward the center. This may be related to the surroundings of the field: marsh and forest. It is likely that moisture levels in the field are highest near the marsh, and decrease with distance from it. Moreover, forest edges have been shown to function as traps for airborne nutrients, leading to higher nutrient deposition in the soil, especially dissolved inorganic nitrogen (Weathers, *et al.* 2002). This may mean that within the field, soil closer to the forest edge had higher nutrient content than soil in the center of the field, accounting for the decreased density and fitness of *B. vulgaris* at the center.

For *S. latifolia*, there was not a significant relationship between density and distance from center, but the average nearest neighbor distance was significantly higher in the peripheral

population, providing limited evidence that distribution is the opposite of what I predicted. This may also be explained by the potentially higher-quality soil at the periphery of the field. With respect to plant fitness, *S. latifolia* showed no relationship between either plant height or flower number and distance from center of the population. This may suggest that fitness is less a product of environmental factors and more a product of inter- and intra-specific competition, as will be discussed later.

I also hypothesized that fitness would increase with population density. For *B. vulgaris*, this pattern was seen in plant height but not flower number. The fact that flower number did not vary with density may be a function of its sexual system. *B. vulgaris* can reproduce both sexually and asexually and is self-compatible (Tachibana *et al.*, 2010), and therefore does not depend on high pollination rates for reproductive success. This means that high density, which generally confers higher pollination success (Kunin, 1997), may not be as important for determining *B. vulgaris* fitness. On the other hand, the fact that height was greater where population density was greater may indicate that where population density is greater, individuals are competing with each other for pollination, as plant height is positively correlated with pollination rates (Mitchell, 1994).

For *S. latifolia*, both plant height and flower number increased as nearest neighbor distance increased. This is contrary to my predictions, and suggests that fitness actually increases as density decreases, which may indicate that intraspecific competition plays a major role in the success of *S. latifolia* individuals. Intraspecific competition has been shown to limit flower number and plant biomass in other flowering species. Ungar (1992) showed that among populations of *Spergularia marina*, there was also a negative relationship between density and flower number, and concluded that this was a result of intraspecific competition. This would also

explain why *S. latifolia* fitness showed no pattern in spatial distribution – if intraspecific competition controls fitness, then fitness would be a function of local density and not overall location within the population.

My two other hypotheses concerned the relative distributions of males and females within the *S. latifolia* population. The ratio of females to males did not differ between central and peripheral portions of the population, which did not support my hypothesis that females would be more abundant at the center of the population. However, flower number for females was positively correlated with distance from the center of the population, despite this trend not showing up for the population as a whole. This is consistent with findings from *B. vulgaris*, that the edges of the field may represent a higher quality environment, which is also consistent with the literature, that females require a more favorable soil requirement than males to support seed production (Freeman *et al.*, 1976).

I also hypothesized that female fitness would increase as distance to the nearest male neighbor decreased. While there was no relationship between female fitness and distance to the nearest male, male fitness increased as distance to the nearest female increased. This may indicate that there is a high degree of intersexual competition between *S. latifolia* individuals. Indeed, Cox (1981) found similar results for *Silene dioica* – among three sampled populations, males that had females as their nearest neighbor had a significantly reduced biomass and number of flowers, which Cox concluded was due to intersexual competition. Eppley (2006) found similar results for a dioecious species of grass, in which she concluded that competitive abilities (i.e. growth and survival rate at high densities) significantly varied between the sexes, leading to mortality disparities and ultimately, very skewed sex ratios. This would explain the extremely

biased sex ratio observed in *S. latifolia*, and may suggest that females have superior competitive abilities over males.

Overall, neither population exhibited an abundant center distribution, and patterns in fitness varied between the two populations. More research is needed on spatial and fitness distribution on the population level – specifically, measuring environmental gradients (in soil moisture, nutrient content, etc.) and their relationship to population density and fitness. Future research should also investigate the nature of intersexual and intraspecific competition within populations of *S. latifolia* to determine the extent to which they impact patterns of spatial and fitness distribution. This study shows that fine-scale patterns in density and fitness may differ from those on the range level, and may be strongly impacted by interactions within species.

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Tables

Table 1. For a population of (a) 196 *Barbarea vulgaris* individuals and a population of (b) 704 *Silene latifolia* individuals, each plant's location was designated as either central or peripheral, and each plant's nearest neighbor was designated as close or far. The relative frequency of individuals with close and far neighbors was compared between the central and peripheral populations.

(a)

	Close Neighbor	Far Neighbor	Total	<i>N</i>
Central	34.29%	65.71%	100%	70
Peripheral	59.52%	40.48%	100%	126
$\chi^2 = 11.467, df = 1, p = 0.0007$				

(b)

	Females	Males	Total	<i>N</i>
Central	67.74%	32.26%	100%	124
Peripheral	67.07%	32.93%	100%	580
$\chi^2 = 0.021, df = 1, p = 0.88$				

Table 2. For a population of 196 *Barbarea vulgaris* individuals, flower number was counted and designated as few or many. The relative frequency of few-flowered and many-flowered individuals was compared between (a) the central and peripheral portions of the population and between (b) individuals whose nearest neighbor was designated as close and individuals whose nearest neighbor was designated as far.

(a)

	Few flowers	Many flowers	Total	<i>N</i>
Central	68.57%	31.43%	100%	70
Peripheral	61.11%	38.89%	100%	126
$\chi^2 = 1.084, df = 1, p = 0.298$				

(b)

	Few flowers	Many flowers	Total	<i>N</i>
Close Neighbor	57.58%	42.42%	100%	99
Far Neighbor	70.10%	29.90%	100%	97
$\chi^2 = 3.28, df = 1, p = 0.068$				

Table 3. For a population of 196 *Barbarea vulgaris* individuals, height was measured and designated as short or tall. The relative frequency of short and tall plants was compared between (a) the central and peripheral portions of the population and between (b) individuals with a nearest neighbor designated as close and individuals with a nearest neighbor designated as far.

(a)		Short	Tall	Total	<i>N</i>
	Central	70%	30%	100%	70
	Peripheral	51.59%	48.41%	100%	126
$\chi^2 = 6.270, df = 1, p = 0.012$					
(b)		Short	Tall	Total	<i>N</i>
	Close Neighbor	45.45%	54.54%	100%	99
	Far Neighbor	71.13%	28.87%	100%	97
$\chi^2 = 13.277, df = 1, p = 0.0003$					

Table 4. For a population of 704 *Silene latifolia* individuals, flower number was counted and designated as either few or many. The relative frequency of few-flowered and many-flowered individuals was compared between (a) the central and peripheral portions of the population and between (b) individuals with a nearest neighbor designated as close and individuals with a nearest neighbor designated as far.

(a)		Short	Tall	Total	<i>N</i>
	Central	59.68%	40.32%	100%	124
	Peripheral	50.34%	49.66%	100%	580
$\chi^2 = 0.021, df = 1, p = 0.059$					
(b)		Short	Tall	Total	<i>N</i>
	Central	55.75%	44.25%	100%	348
	Peripheral	48.31%	51.69%	100%	356
$\chi^2 = 3.895, df = 1, p = 0.048$					

Table 5. For a population of 704 *Silene latifolia* individuals, height was measured and designated as either short or tall. The relative frequency of short and tall individuals was compared between (a) the central and peripheral portions of the population and between (b) individuals with a nearest neighbor designated as close and individuals with a nearest neighbor designated as far.

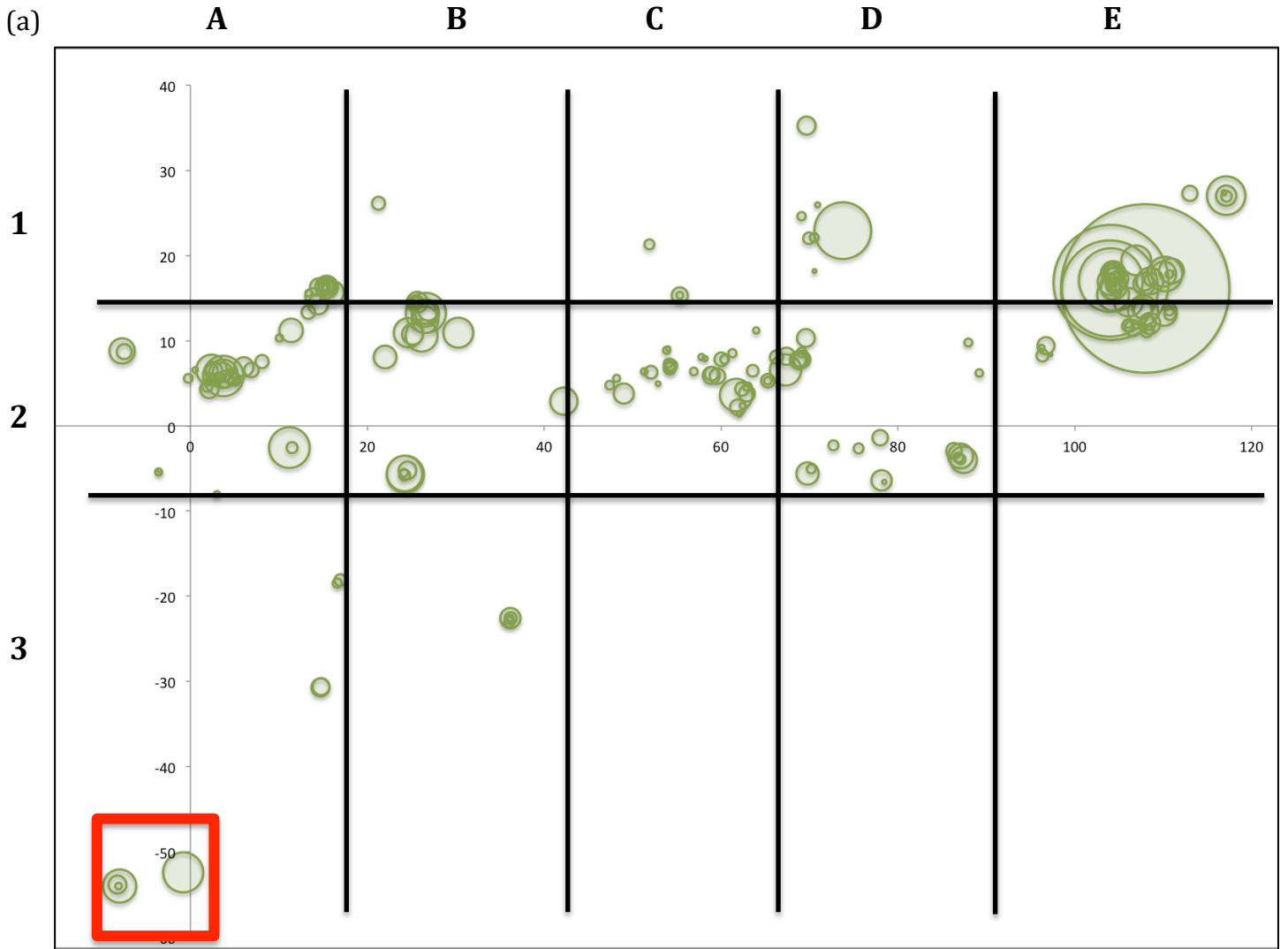
(a)

	Short	Tall	Total	<i>N</i>
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Peripheral	50.34%	49.66%	100%	580
$\chi^2 = 0.021, df = 1, p = 0.059$				

(b)

	Short	Tall	Total	<i>N</i>
Central	55.75%	44.25%	100%	348
Peripheral	48.31%	51.69%	100%	356
$\chi^2 = 3.895, df = 1, p = 0.048$				

Figures



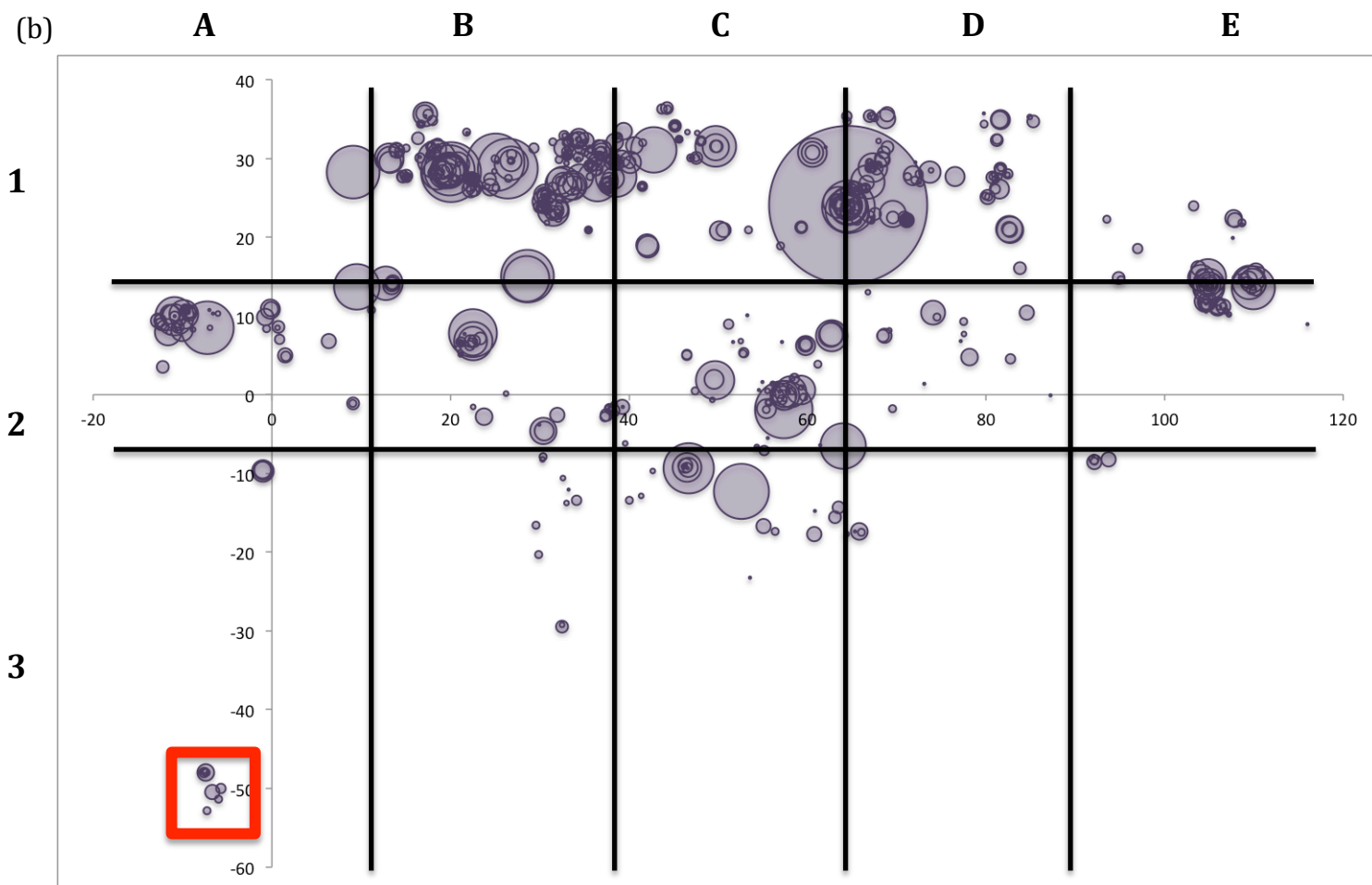
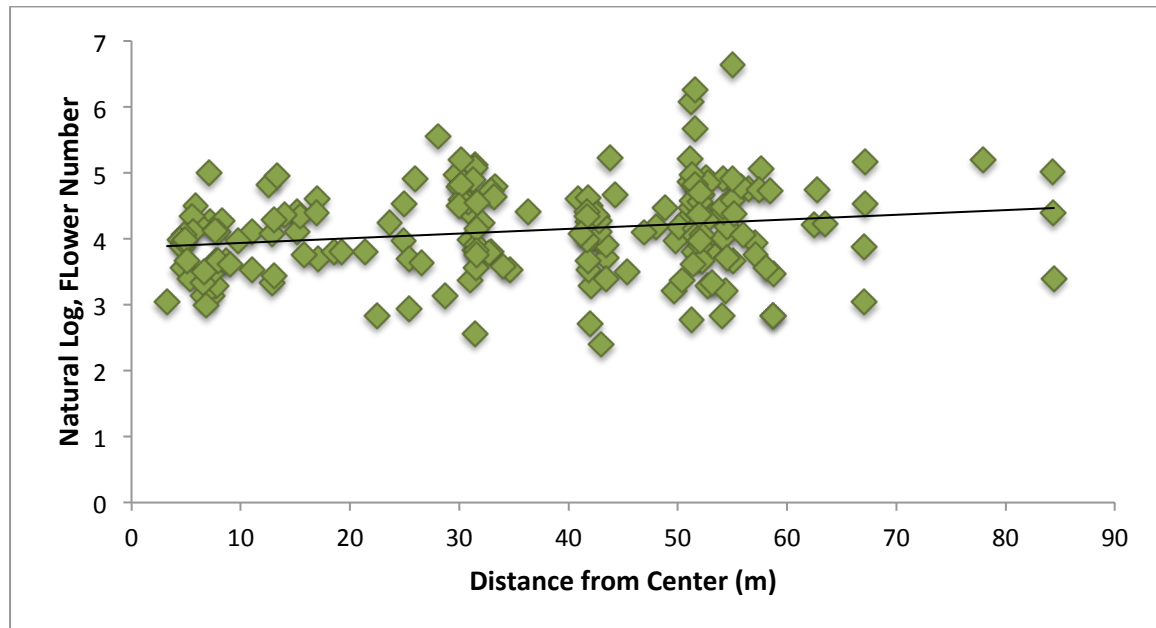


Figure 1. *B. vulgaris* (a) and *S. latifolia* (b) distribution. Individuals are shown as circles with diameters weighted according to flower number. In order to classify individuals as central or peripheral, the x-value range was divided into five parts and the y-value range into three. Individuals that fell within the coordinates (B, 2), (C, 2), or (D, 2) were considered central, and the rest were considered peripheral. Note that individuals in the red squares were treated as geographic outliers and their coordinates were not included when determining central and peripheral areas.

(a)



(b)

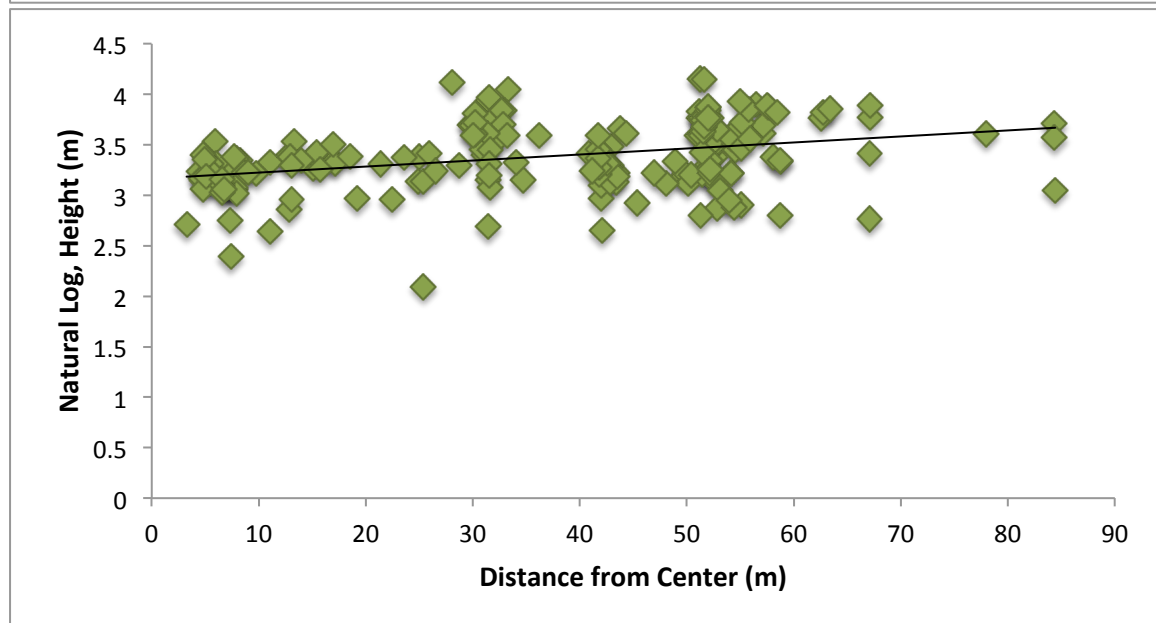


Figure 2. The number of flowers and plant height (cm) for 196 individuals of *Barbarea vulgaris* were recorded during the summer of 2014. Distance (m) was measured from the center of the population. (a) *B. vulgaris* flower number vs. distance from center ($R^2 = 0.0481$, $df = 194$, $p = 0.002$). (b) *B. vulgaris* height vs. distance from center ($R^2 = 0.1217$, $df = 194$, $p < 0.0001$). Both height and flower number were transformed to their natural log.

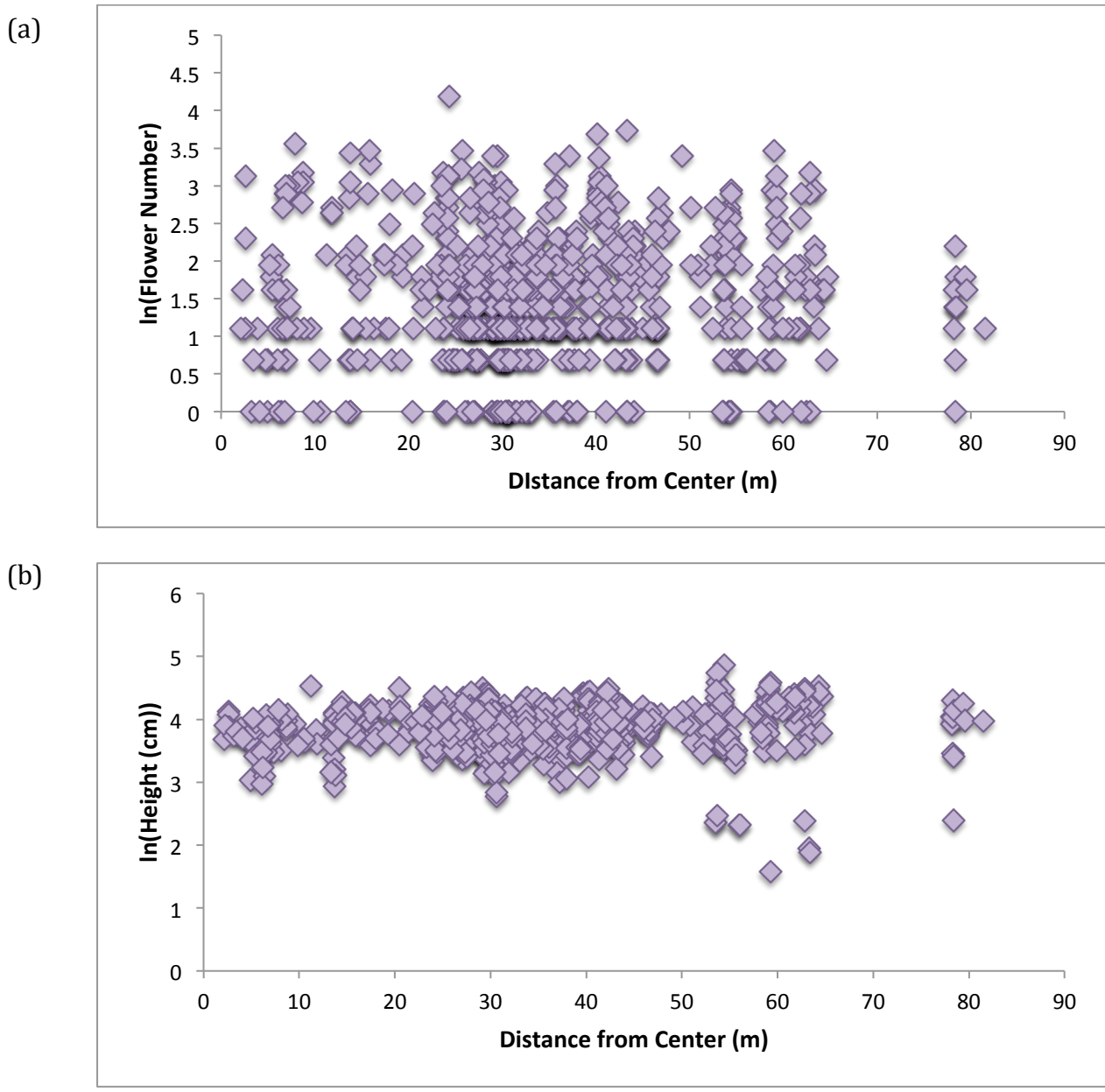


Figure 3. The number of flowers and plant height (cm) for 704 individuals of *Silene latifolia* were recorded during the summer of 2014. Distance (m) was measured from the center of the population. (a) *S. latifolia* flower number vs. distance from center ($R^2 = 0.0003$, $df = 702$, $p = 0.624$). (b) *S. latifolia* height vs. distance from center ($R^2 = 0.0054$, $df = 702$, $p = 0.062$). Both height and flower number were transformed into their natural log.