

CLINAL DIFFERENTIATION AND PUTATIVE HYBRIDIZATION IN A CONTACT ZONE OF *PINUS PONDEROSA* AND *P. ARIZONICA* (PINACEAE)¹

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The widely distributed *Pinus* subsection *Ponderosae* is a species complex that has a transition zone among taxa in the southwestern United States. In southern Arizona and New Mexico at least two recognized taxa, *Pinus ponderosa* var. *scopulorum* and *Pinus arizonica* or *P. ponderosa* var. *arizonica*, are known to coexist in close proximity. In this study, we report the existence of populations where the taxa are sympatric. One of the key characteristics distinguishing taxa is the number of needles per fascicle; *P. ponderosa* typically has three, *P. arizonica* has five. We examined the spatial distribution of needle-number types in a belt transect that covers a transition zone from nearly pure three-needle types at the top of Mount Lemmon to five-needle types downslope, in the Santa Catalina Mountains, Arizona. The spatial distribution is inconsistent with there being both free interbreeding among types and selective neutrality of types. Trees with intermediate types, having combinations of three, four, and five needles and/or mean numbers of needles between 3.0 and 5.0, are spatially concentrated in the middle of the transition zone. The spatial distribution supports the occurrence of hybridization and introgression, and this is consistent with reported crossabilities of the types. The results suggest that selection is acting, either on needle number per se or on other traits of the ecotype with which it may be in linkage disequilibrium, to maintain the observed steep clinal differentiation.

Key words: clinal differentiation; contact zone; hybridization; Pinaceae; *Pinus arizonica*; *Pinus ponderosa*.

Pinus ponderosa has a broad distribution across much of the montane western United States. It is considered to be exceptionally widely adapted (e.g., Conkle and Critchfield, 1988), and a number of regionally adapted ecotypes have been identified. These types have been variously classified as races, varieties, forms, or as separate species, but all are placed in the subsection *Ponderosae*. Hybridization is widespread among the taxa (Conkle and Critchfield, 1988). In the southwestern United States, populations exist in a transition zone. The distribution of *Pinus ponderosa* extends south along the Rocky Mountains and to the broad plateau country in northern Arizona and New Mexico, where it is generally considered to consist of the taxon *Pinus ponderosa* var. *scopulorum* Engelm. In Mexico, several other taxa exist in the Sierra Madre, and some of these extend northward up to the southern border of Arizona and New Mexico. Most notable among these is one type originally identified as *Pinus arizonica* Engelm. or *Pinus ponderosa* var. *arizonica* (Engelm.) Shaw. In the southern third of Arizona and New Mexico, *Ponderosae* populations are small and scattered, confined to mountaintops. Taxa in this

area have been classified in various ways (see review by Rehfeldt, 1999), but there are at least two taxa, which differ markedly by a variety of morphological traits (Rehfeldt et al., 1996). Nonetheless, the taxa hybridize well in controlled crosses (Conkle and Critchfield, 1988).

Populations in the Santa Catalina Mountains, north of Tucson, Arizona, are of particular interest. *Ponderosae* are known to have persisted there, and perhaps nowhere else in the region, during the Wisconsin glacial era (Van Devender, 1990). The Santa Catalina Mountains contain at least two different taxa of ponderosa pine (*Ponderosae*), originally classified as the Rocky Mountain variety, *P. ponderosa* var. *scopularum*, and the Arizona pine, *P. arizonica* or *P. ponderosa* var. *arizonica* (Kearney and Peebles, 1960). Rehfeldt (1999) presents detailed information on the distributions of different morphological types in the southern regions of Arizona and New Mexico, including the Santa Catalina Mountains. The types differ for a variety of traits, including genetically based differences in numbers of needles per fascicle and needle length, and various seed cone and shoot elongation traits (Rehfeldt, 1999). Needle number per fascicle is a key characteristic with high heritability. The *P. ponderosa* var. *scopularum* type typically has three needles per fascicle (although it often has two needles in the Rocky Mountains), whereas *arizonica* typically has five needles.

We have found a number of transitional populations in the Santa Catalina Mountains. Field observations on the distribution of the *Ponderosae* based upon needle number per fascicle report the existence of a relatively pure stand of the three-needed variety on the summit (2791 m) and north slope of Mt. Lemmon and a mix of three- and four-needle pines on the summits of Mt. Kellogg (2605 m) and Mt. Bigelow (2605 m). The lower elevations, especially on the lower flanks of Mt. Lemmon and into the Wilderness of Rocks region, below 2438

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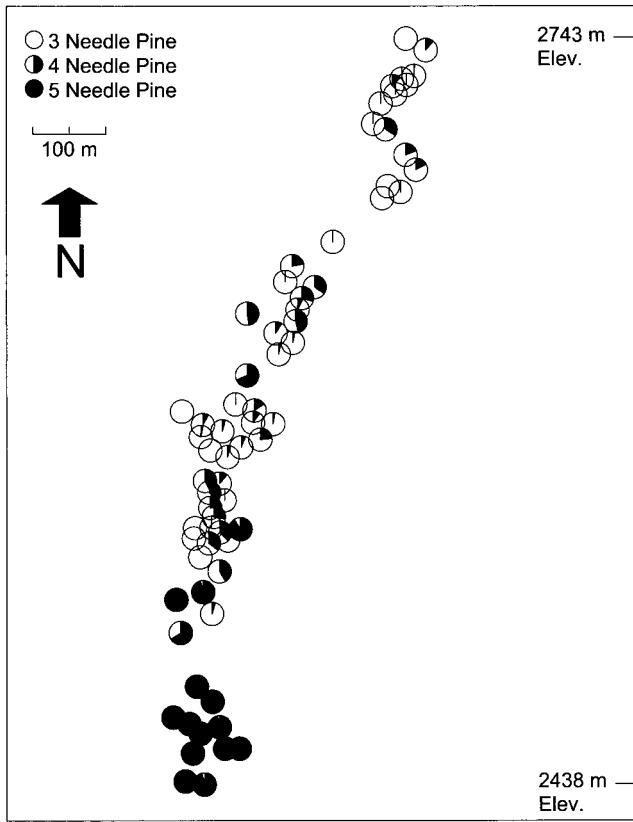


Fig. 1. Distribution of sampled trees, with their mean numbers of needles per fascicle, in the belt transect. The percentage of fill in each pie diagram indicates the excess of the mean, Z , beyond 3.0, i.e., is equal to $(Z - 3)/2$. For example, a tree with a mean of 5.0 is represented by a completely filled pie, 4.0 by half-filled, and 3.0 empty.

m in elevation, are dominated by trees possessing primarily five needles per fascicle (F. W. Telewski, unpublished data). In between these two extremes we found trees containing a mix of three, four, and five needles. It has been suggested that such intermediate trees may represent hybrids between the two taxa (Peloquin, 1984) or alternatively a separate taxa (Rehfeldt, 1999). The purpose of the present study was to examine the population structure and spatial distribution of needle types in populations of *Ponderosae* along an elevational gradient where the two taxa are sympatric and possibly hybridizing.

MATERIALS AND METHODS

Seventy-one cone-bearing trees within the *Ponderosae* were sampled in September 1996 along an elevational gradient beginning at 2743 m on the south slope of Mt. Lemmon, Santa Catalina Mountains, Pima County, Arizona, and extending down to an elevation of 2438 m (Fig. 1). This gradient included the transition from a primarily three-needle-leaved population of ponderosa pine (*Pinus ponderosa* var. *scopularum*) at the summit of Mt. Lemmon to a primarily five-needle-leaved population (*Pinus ponderosa* var. *arizonica* or *Pinus arizonica*) at 2438 m in elevation. The belt transect had approximate dimensions, measured in horizontal distances, of 1.0 km \times 100 m, or an area of \sim 10.0 ha. The average slope was \sim 30%. Criteria for selection of sampled trees included the availabilities of collectable mature green cones (using a pole-pruner with 10 m maximum extension) and a minimum of three branches for needle counts. Sampled trees were measured for diameter at breast height (dbh; i.e., at height \sim 147 cm) and marked using num-

bered aluminum tags. Among sampled trees, all individuals exceeded 20 cm dbh, although dbh was not a criterion for selection.

Global positioning satellite (GPS) coordinates were obtained for each sampled tree using a high-resolution Trimble GeoExplorer Model 17319–32 unit with calibration base station (U.S. Forest Service, Santa Catalina Ranger District, Coronado National Forest). Field coordinates were recorded in Universal Trans-Mercator (UTM) units, calibrated, and plotted using ArcView geographic information system (GIS) software.

The numbers of needles per fascicle were counted and tabulated for several hundred fascicles from three branches from each tree. Care was taken to determine the exact number of needles per fascicle, accounting for broken, missing, malformed, or aborted needle leaf formation within each fascicle. This was accomplished by observing the formation of a cylinder of foliar tissues within the fascicle sheath.

In order to obtain a rough estimate of the density of *Ponderosae* in the sample area, we set up 16 plots at locations more or less evenly spaced, but otherwise randomly located, along the belt transect. For each plot we counted all *Ponderosae* within an 8-m radius and measured their diameters at breast height. A few individuals were found with heights $<$ 147 cm, and these were simply recorded as "seedlings."

The mean number of needles per fascicle and its standard error (SE) were calculated for each of the 71 trees using SAS procedure *Means* (SAS, 1982). Spatial autocorrelation was characterized and quantified using standard (unweighted) Moran's *I* statistics (Sokal and Oden, 1978; Cliff and Ord, 1981), separately for the means and standard errors. Each pair of trees was considered as a join and assigned to one of a number of mutually exclusive distance classes. Three different sets of distance classes were formed in separate analyses. Each set of distance classes was formulated so that there were similar numbers of pairs for all distance classes; this designation produces favorable statistical properties (e.g., Epperson, 1993). For each analysis, Moran's *I* values (Sokal and Oden, 1978) were calculated for each distance class, using the standard formula:

$$I = \frac{n \sum_{i=1}^n \sum_{j=1}^n w_{ij} Z_i Z_j}{W \sum_{i=1}^n Z_i^2} \quad (1)$$

where n is number of individuals (71); w_{ij} is an element of the weighting matrix, such that w_{ij} equals 1.0 if i th and j th individuals are in the distance class and zero otherwise; W is twice the total number of pairs for the distance class; $Z_i = X_i - \bar{X}$, $Z_j = X_j - \bar{X}$; the variables X_i and X_j are the values for the trait (either the mean number of needles per fascicle or its SE) for i th and j th individuals, respectively; and \bar{X} is the grand mean value for all individuals in the sample. Each *I* value was tested for significant deviation from the expected value, $E(I) = -1/(n - 1)$ under the null hypothesis of a spatially random distribution (Cliff and Ord, 1981). A significant positive value of Moran's *I* indicates that pairs of individuals in the distance class considered have similar or correlated values of the trait, whereas a significant negative value indicates that they have dissimilar values. In addition, each set of *I* statistics for mutually exclusive distance classes, known as an *I* correlogram, was tested for statistical significance, using Bonferroni's criteria (Sakai and Oden, 1983). All spatial autocorrelation results were obtained using Wartenberg's SAAP (version 43) computer program. Distance classes were based on the Euclidean horizontal distance between pairs of trees, estimated using Universal Trans-Mercator (UTM) coordinates obtained through the GPS data gathered at the field plot. Because the area is small, the distance values correspond closely to meters.

RESULTS

Figure 2 shows the *I* correlogram for the mean number of needles per fascicle for one set of distance classes. It indicates a very high level of spatial autocorrelation. All of the individual *I* statistics were statistically significant at the 1% level, and the overall *P* value for the *I* correlogram was <0.001 . There

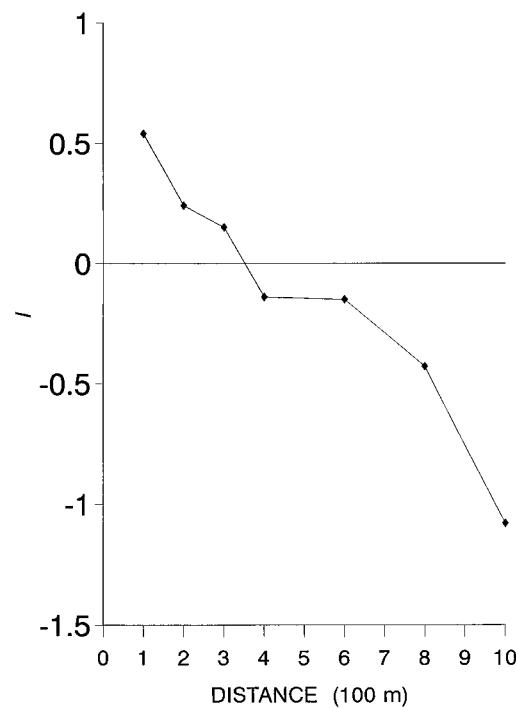


Fig. 2. Correlogram of Moran's autocorrelation statistic, I , as a function of distance, for the mean number of needles per fascicle for individual trees.

are very high positive values for short distances, up to distance class 3 (upper bound 300 m), and large negative values at larger distances. Interpolating between distance classes 3 and 4 provides an estimate of ~ 350 m for the intercept. There is a very high degree of correlation at short distances, and the correlation drops off smoothly as distance increases. Moreover, the pattern of large negative values for long distances, which continue to decrease to the limits of the sample distances, is striking. The statistics computed for other sets of distance classes are not shown because they are redundant with those in Fig. 2. In sum, the results show a very strong cline in needle number roughly centered at the center of the sample area, and the orientation of the cline, clearly indicated by inspection of the data, is with three-needle pines at the higher elevation end of the sample area and five-needle pines at low elevations.

Figure 3 shows the autocorrelation statistics for the standard errors in needles per fascicle for individual trees for a slightly different set of distance classes. There is very little autocorrelation. In this set, only one negative statistic (for distance class 5, for distances >529 m but ≤ 662 m) and one large positive value for the greatest distance class (distances >1059 m) were statistically significant, and the overall P value is 0.023 for the correlogram. All of the statistics for both of the other two sets of distance classes employed were not significant. Nonetheless, there is a strong pattern, reflected by the positive value at long distances, in that opposite (3 vs. 5) "pure" or nearly pure types are concentrated at the two ends of the sample transect, and individuals of both types have very low variances in needle numbers. There is a strong, highly nonlinear association of mean needle number with standard errors (Fig. 4). Consequently, even though the means and variances are associated, spatial autocorrelation in the former does not cause autocorrelation in the latter. Overall, the results for the spatial correlograms fit with inspection of the distribution,

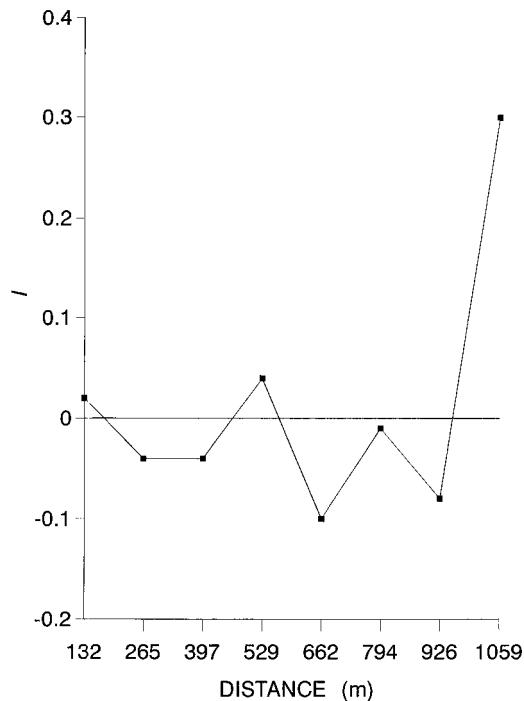


Fig. 3. Correlogram of Moran's autocorrelation statistic, I , as a function of distance, for the standard error of the mean number of needles per fascicle for individual trees.

in that individuals with higher variances (and intermediate mean numbers of needles) are highly concentrated into the center of the sample area.

A total of 204 *Ponderosae* individuals were counted in the density plots, and only ten of these were classified as "seed-

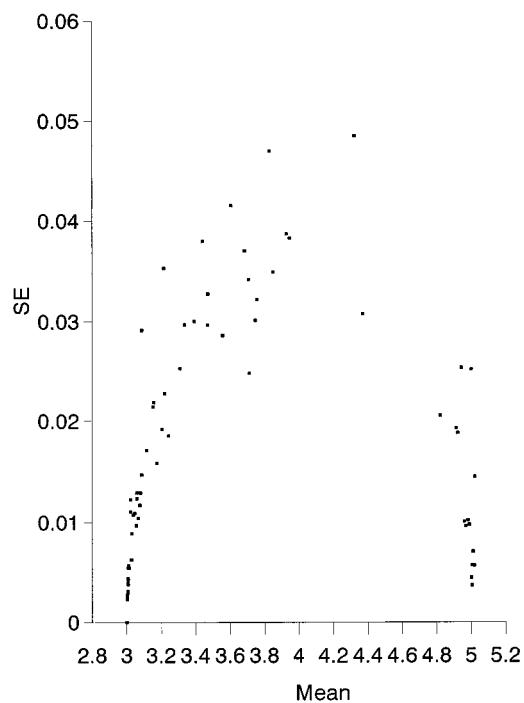


Fig. 4. Scatter plot showing the relationship of the mean number of needles per fascicle to its standard error, among individual trees.

lings" (<147 cm tall). The mean was 12.75 individuals of *Ponderosae* species per plot (0.0201 ha). The numbers ranged from 1 to 33, the standard deviation was 9.6. Hence the estimated standard error was 2.4, and the 95% confidence interval was 8.03–17.47 individuals per plot. The number (65 total) of trees with dbh greater or equal to 20 cm ranged from one to nine per plot, with a mean of 4.06, standard deviation 2.21, standard error 0.55, and 95% confidence interval of 2.98–5.14. Thus, our point estimates are precise to within ~25–30%. Based on the point estimates there were ~634 individuals per ha and for trees with dbh 20 cm or greater there were ~202 individuals/ha.

Based on density estimates and the plot size, the sample represents an intensity of ~71/(10.0 ha × 634/ha) = 1.1% of the total *Ponderosae* individuals or 71/(10.0 ha × 202/ha) or 3.5% of the age class that is likely to contain cones.

DISCUSSION

A very high degree of autocorrelation was observed for the average number of needles per fascicle among trees in the belt transect. Indeed, the observed values of Moran's *I* statistics are among the highest ever observed for genetic traits in any species (Epperson, 1993), and they are much higher than would usually be expected for selectively neutral traits in a species like ponderosa pine. The values are large enough that there seems to be only two possible explanations. One is that the contact between the needle types has occurred very recently and happened in a particularly constrained way. The other, which is arguably more likely, is that either the five-needle trait itself or the ecotype it characterizes is selectively favored at lower elevations, with the three-needle form favored at higher elevations along the transect.

To understand just how large the observed autocorrelation is we can compare it to the expected value based on how far seed and pollen disperse in a freely interbreeding population (Sokal and Wartenberg, 1983; Epperson, 1990; Epperson and Li, 1997). Ponderosa pine seed and pollen disperse relatively long distances (Epperson, 1992). Pine seed usually have dispersal distances such that the axial variance distance (formally, the variance in the distance dispersed measured along one of two axes in two-dimensional space), σ_s^2 , is in the range of ~289–2500 m² (e.g., see Epperson and Allard, 1989), and in ponderosa pine estimates of seed dispersal variance average 1369 m² (Govindaraju, 1988). Similarly, pine pollen has axial variance distances, σ_p^2 , of ~289–4225 m² (e.g., Wright, 1976). Thus, Wright's neighborhood area should be in the range of 1.9–4.4 ha, using Wright's (1943) formula ($N_a = 4\pi\sigma_i^2$), and Crawford's (1984) formula ($\sigma_i^2 = \sigma_s^2 + \sigma_p^2/2$). The point estimates of density were 634 total ponderosa per hectare and 202 ponderosa trees per hectare with dbh 20 cm or greater. Using conservative estimates of 202 trees per hectare, Wright's neighborhood size must exceed 384 (1.9 × 202). Using this value, and a conservative estimate of 1 in 25 for the sampling intensity, and interpolating from Table 4 of Epperson, Huang, and Li (1999), the predicted value of Moran's *I* statistic is ~0.01 for distance class 1. Use of a larger value of density or a smaller percentage of individuals sampled would give even smaller predicted values. Thus, the observed value is at least 50 times larger than that predicted for a freely interbreeding population. Moreover, in qualitative terms this is the difference between a nearly maximally structured population (0.5) and a nearly random distribution (0.01). The observed spatial dif-

ferentiation is inconsistent with the idea that the population in the area is a single interbreeding population.

It is important to note a few additional considerations when comparing the data to simulation studies. First, most of the simulation results are for single-locus genotypes, but results for multilocus traits indicate that the same correlations are expected for the genetic component of most quantitative traits (Epperson, 1995). Moreover, single-locus traits and the genetic component of quantitative traits should also have similar spatial distributions when considered on much larger spatial geographic scales (Rogers and Harpending, 1983). As noted in the introduction, there is a large genetic component to needle number variation in ponderosa pine (sensu lato) (Rehfeldt, 1999) and an environmental component. Rehfeldt found that needle number has an individual heritability of ~60%. An environmental variance component adds spatially random "white-noise" to a spatial pattern of genetic variation, and thus would tend to cause, if anything, a decrease spatial autocorrelation, implying that the genetic component has even stronger spatial autocorrelation than that we observed for the phenotypes. Thus, we may conclude that the spatial autocorrelation of genetic variation for needle number in the study population is much larger than that expected for neutral traits in a single population.

It appears that the only way that neutral theory can explain the observed pattern is if the contact is very recent and populations of the two types came into contact as nearly intact, i.e., as nearly pure blocks. This in itself seems rather unlikely because dispersal distances of individual seed is highly variable, and thus one would expect more spatial mixing as the populations spread toward each other. Moreover, if the two types interbreed, then pollen movement variations would also soften any spatial boundaries. The presence of intermediate types suggests that there is some hybridization. The needle number data are extensive. For example, for some "pure three-" needle trees every one of the several hundred scored fascicles had three needles. The differences in needle number and standard errors among the trees are characteristic, not statistical. The fact that there are pure trees of both types and intermediate types (also with larger standard errors) suggests that there are hybrids and possibly backcrosses. Thus, the neutral theory appears to also require that the present generation must be essentially the first generation after contact, that there was little or no cross-pollination in prior generations and little or no spatial mixing of seeds. The first requirement seems unlikely because at least some *Ponderosae* have been in the Santa Catalina Mountains during the Wisconsin glaciation, and the latter seems unlikely given that seed and pollen can disperse 50 m or more. Our data do not allow distinction of whether it is the needle number itself which is selected or whether it is because of linkage disequilibrium with other traits of the ecotypes. Either way, it seems likely that parental types have not survived well on the opposite parental type location (e.g., three-needle types have not survived well downslope, i.e., on the five-needle type location), and that hybrids and backcrosses have not survived well on both parental type locations (represented by the bottom and top of the transect area).

It should also be noted that the *I* statistics for large distance classes had very large negative values and such are not observed for neutral traits in populations at equilibrium. In other words, in addition to consideration of magnitudes of individual *I* statistics, the shape of the *I* correlograms is different. Normally, we should use considerable caution in interpreting *I*

statistics for long distances, but the trend is sufficiently striking in ponderosa pine that we may conclude it is clearly different from neutral theory. Moreover, the only theoretical I correlograms like the observed ones that have been generated to date were produced by clines in response to microenvironmental selection gradients (Sokal, Jacquez, and Wooten, 1989).

The variance in needle number is small for trees that have an average near either 3.0 or 5.0 needles. This suggests that these trees are pure types, uninfluenced by introgressed genes from the opposite type. It also suggests that needle number is tightly controlled or highly canalized in pure types. In contrast, individuals with intermediate numbers of needles, i.e., those with an individual average in the range of ~3.5–4.5 have much larger individual variances. It is interesting but speculative to note that the apparent hybrid individual may be less canalized with respect to needle primordia formation.

As noted, the presence of three types of trees in juxtaposition—pure three needle, pure five needle, and trees with intermediate needle numbers—strongly suggests hybridization is occurring, as well as possibly advanced introgression. However, Rehfeldt (1999) has argued against hybridization, in part relying on the claim that the two types are allopatric. Nonetheless, reproductive compatibility between the taxa has been demonstrated (Conkle and Critchfield, 1988). However, Rehfeldt (1999) suggests that there may be phenological differences based on indirect evidence of juvenile vegetative shoot elongation, although other authors have examined geographic distributions and concluded that there is extensive hybridization in the region (Peloquin, 1984). We have not observed detailed phenologies of flowering times; however, it seems unlikely that this could result in complete reproductive isolation, because there are likely to be phenological differences associated with microclimate changes along the steeply sloped transect, and pollen can move throughout the transect area. We have observed differences in seed cone maturation dates along the transect. Rehfeldt (1999) also suggests that there are strong differences between the microhabitat requirements of the two taxa. Our results support this as a general feature, but they also support the occasional formation of hybrids that are in turn reproductively successful within the contact zone. Moreover, trees with needle numbers continuously spanning the range of 3.0–5.0 needles are represented in the transect area, including some individuals with needle numbers close to 4.5, i.e., intermediate between 4 and 5. This also strongly suggests that hybrids and various later generation crosses (including both backcrosses) have occurred with some frequency. More of the intermediates have <4.0 needles (mean) than have >4.0 needles (mean), but this could be due either to partial dominance or to what would be expected if the five-needle taxon has been expanding up the mountainside (discussed below). In addition, it is worth noting that only older trees contribute much to female reproduction, so that hybrids would most likely first function as males pollinating female cones of three-needle trees.

A closer examination of the spatial distribution provides further evidence for hybridization. While five-needle trees are clearly spatially constrained to the bottom of the transect and three-needle trees dominate the top, the intermediate types are mixed with the three-needle types in the middle of the transect. To exclude the marked effects of the five-needle trees, we conducted a further spatial autocorrelation analysis after excluding all individuals with ≥ 4.6 needles (mean) (following the Peloquin's [1984] definition of a "five-needle type").

Moreover, this allows us to test Rehfeldt's (1999) specific idea that there exists a "taxon X," a primarily three- and four-needle taxon. We found the following values of Moran's I statistics: 0.02, -0.02, 0.03, -0.04, 0.01, -0.15, for the first six of the same seven distance classes as in Fig. 2. The values for short distances are much smaller than those for the full data set (e.g., 0.52 for distance class 1), and this shows that the various non-five-needle types are indeed highly mixed over short distances. However, there is a very large negative value (-0.15) for long distances (600–800 m) which indicates strong differentiation over this part of the transect. Inspection of the surface (Fig. 1) clearly indicates the orientation of this differentiation: trees with needle numbers nearer to 3.0 occur on the top, whereas trees with higher values are concentrated 600–800 m down the mountainside. In other words, the spatial center of the intermediate types is precisely in the middle of the two pure types. This nonrandom pattern suggests that these types are hybrids or advanced introgressed types.

It could be argued that needle type is plastic and responsive to differences in the environment along the transect, but this contradicts the large genetic component observed (Rehfeldt, 1999). Moreover, if higher temperatures increased needle numbers down the mountainside, then why are large mature trees with means of 3.0 (and standard errors 0.00) found in the middle of the transect? Regarding the spatial distribution of such inferred genetic variation, though it may fit expectations for the shortest distance classes, the spatial distribution at longer distances (particularly the concentration of types with relatively higher needle numbers in the middle of the study area) does not fit with expectations for a single interbreeding population of three- and four-needle individuals.

Finally, the size structure of the trees suggests that the five-needle types are spreading their genes up the mountainside. Trees with needle numbers near 3.0 have a wide range of sizes (and hence ages) on the mountaintop, but those near the middle of the transect are nearly all very large individuals. For example, the median dbhs of three-needle individuals (mean needle number <3.20) at 0–250, 251–500, and 501–750 m from the top of the transect are 28.5, 30.9, and 44.8 cm (interpolated from even-number samples), and the means are 30.0, 32.5, and 45.9, respectively. It is worth pointing out that temperature increases over the past few hundreds of years could be shifting the suitable habitat for the five-needle eco-type up the mountainside. The five-needle form is likely to be more adapted to hot and dry conditions. The spatial pattern itself also suggests that the five-needle types and/or their genes are moving up the mountainside, more so than the three-needle type genes moving downslope.

The observed distribution of needle numbers characteristic of pure types and intermediate types strongly suggests that hybridization and substantial introgression have occurred. However, further analysis of molecular markers and age structure may allow more detailed conclusions about the precise nature of the hybridization and introgression in such contact zones.

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