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A spatially explicit census reveals population structure and recruitment patterns for a narrowly endemic pine, *Pinus torreyana*

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20 **Abstract** We conducted a census of the rare pine, *Pinus torreyana* ssp. *torreyana,* in order to
21 determine: a) what is the population size and is it stable, growing or declining; b) what is the
22 spatial variation in population structure; c) what is the spatial patterning of trees in different life
23 stages; and, d) what environmental factors are related to seedling recruitment? Trees were
24 classified into four stages classes: adult (> 160 cm tall with cones); sub-adult (> 160 cm without
25 cones); saplings (30-160 cm), and seedlings (< 30 cm). Stem diameter was measured for adults
26 and sub-adults, and height for saplings and seedlings. Stands were defined by spatial clustering
27 of the tree map. Univariate and bivariate point pattern analyses were used to explore spatial
28 patterns for adult and juvenile trees and identify potential stand development processes such as
29 density dependence, dispersal limitations, and patchy recruitment. Logistic regression was used
30 to analyze seedling establishment and survival in relation to environmental variables derived
31 from digital maps. We expected to find little or no recruitment based on earlier studies. Instead,
32 5422 trees were mapped and measured, and tree size had "reverse J-shaped" distribution
33 suggestive of a recruiting population. However, population structure was variable among stands.
34 The predominant spatial pattern detected for adult and juvenile trees was clustering at lag
35 distances < 10 m. Bivariate pattern analysis did not suggest repulsion between adult and juvenile
36 size classes. Seedlings tended to be found close to adults and on certain soil types. Taken
37 together, this suggests that the clustered patterns resulting from patchy recruitment and survival
38 of juveniles persist over time.

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Introduction

While an important aspect of species conservation is identifying critical habitat encompassing key populations of threatened species and protect them within a reserve system (Groves et al. 2002), preserving habitat may not be enough to ensure long term persistence of an already stressed species (Knight et al. 2006; Margules & Pressey 2000). Management action may be required to prevent further decline in a population by eliminating environmental threats or initiating active restoration. However, a lack of basic demographic data leads to uncertainty regarding management of endangered species (Noss 1999). It is often necessary to collect data including size and age structure of populations, species life history characteristics, and rates of change in abundance and range in order to estimate extinction risk and identify threats and potential management actions (Keith 2000). With a small, locally restricted plant population, the most comprehensive assessment approach involves a census incorporating all life history stages and tracking individuals over time (Schemske et al. 1994). In long lived species population change is slow and can be difficult to detect, and when longitudinal studies are not feasible, an assessment of the population's age structure can be used to infer status and trends (Newton 2007).

In this study we demonstrate that a spatially explicit census, in which individuals are enumerated and mapped, is feasible and informative for a rare, long lived plant species, allowing spatial heterogeneity in the population to be detected and related to environmental gradients and historic processes (past disturbance). We will show that while a census can, of course, reveal population size and structure, a population map can be used to determine spatial variation in age structure, recruitment, mortality, and in the spatial association of juveniles and mature individuals. This allows spatial variation in processes affecting the population (dispersal, seed predation, recruitment, competition) to be inferred so that management can occur at an appropriate scale.

The focus of this study, *Pinus torreyana* C. Parry ex Carriere ssp. *torreyana,* is a tree species endemic to southern California and listed as rare, threatened and endangered by the California Native Plant Society (http://cnps.org/cnps/rareplants/inventory/, accessed 9/20/09). Even with a large portion of its natural range under protected status, the mainland population of *P. torreyana* is both surrounded and fragmented by urban development, and is exposed to many potential threats including historic habitat loss, altered fire regime, climate change, exotic competitors, pests, disease, and recreational land use. Previous studies raised concern that the population may be in decline because little seedling recruitment was observed and the age structure suggested an aging population. However, the lack of comprehensive demographic data has lead to uncertainty regarding the status of the population and consequently monitoring and management needs.

With a variety of potential threats to *P. torreyana,* it is important to manage the population in order to minimize those risks. However, in order to do so there must be a solid understanding of the current status and trends of the population. In this study we addressed the

83   basic but unanswered questions about this iconic species: a) what is the population size and is it
84   stable, growing or declining (inferred from size structure); b) what is the geographical variation
85   in population structure; c) what clues about population dynamics can be found in the spatial
86   patterning of trees in different life stages; and, d) what environmental factors are related to
87   seedling recruitment?

88

89   **Methods**

90   Study Species

91   *P. torreyana* is found naturally in only two geographically isolated locations. The mainland
92   population, *P. torreyana* ssp. *torreyana*, occurs along a narrow strip of Southern California coast
93   immediately south of Del Mar, California, USA (Haller 1986). The study population is found
94   within Torrey Pines State Reserve (TPSR; 590 ha). Another subspecies, *P. torreyana* ssp.
95   *insularis*, is found on Santa Rosa Island in the Santa Barbara Channel. Within the TPSR, *P.
96   torreyana* is distributed across varied terrain, associated with loose sandstone soils (Haller 1986),
97   and seemingly absent on the richer shale soils (Cario 1996).

98   In order to account for the species' lack of genetic diversity, Ledig and Conkle (1983)
99   propose that *P. torreyana* may have gone through a population bottleneck approximately 3000
100   years ago; they also reported that the current population size of *P. torreyana* was unknown but
101   speculated to be about 6000-7000 individuals. The present population may be at its highest adult
102   numbers in the last several thousand years based on palynological evidence and historical air
103   photos (Cole & Wahl 2000). More recently, between 1988 and 1993 about 840 trees were killed
104   by infestation of drought-weakened trees by the bark beetle, *Ips paraconfusus*. Deployment of
105   pheromone-baited funnel traps that greatly reduced the infestation and halted additional tree
106   death (Shea & Neustein 1995).

107   Age distribution in *P. torreyana* in TPSR was investigated by McMaster (1980) based on
108   cores from 85 trees and he reported a mean age of 78 (+/-25) yr, ranging from a mean of 62 to 92
109   yrs in stands with different disturbance histories. McMaster only observed three individuals in
110   the 2-30 yr age group which suggested poor recruitment during the three decades preceding the
111   study. Wells & Getis (1999) reported similar results after surveying a one-ha plot of mature
112   trees; observed size distribution was skewed to larger size (age) classes and there was a complete
113   absence of juvenile recruitment. The square root of the diameter at breast height (DBH) was
114   used as surrogate for age in that study based on an empirical correlation ($R^2 = 0.736$).

115   In contrast to the lack of recruitment in undisturbed areas, locations with more recent
116   disturbance such as fire had experienced significant recruitment of *P. torreyana*. Seven years
117   following an arson-ignited fire that killed 93 adult Torrey pines in an area called East Gove, 220
118   juvenile pines were counted in a 7.7 ha stand (McMaster 1980; Wells & Getis 1999). There
119   were also modest gains in recruitment following prescribed burns in the same area in 1984 and
120   1985, resulting in three distinct age cohorts (Wells & Getis 1999).

121   Germination and seedling survival appear to be limited by heavy ground litter and
122   competition from shrubs (Cario 1996; Wells & Getis 1999). Although above average rainfall
123   results in high seedling recruitment levels in *P. torreyana*, first-year seedling survival rates has
124   been found to be low (0-28%), and water stress during hot dry summer months is identified as
125   the leading cause of seedlings mortality (Cario 1996; McMaster 1980). Spatial pattern analysis

126 revealed that in East Grove *P. torreyana* did not recruit under the canopy of adult trees, rather
127 young trees recruited in open areas and followed the expected pattern of spatial clustering up to a
128 critical distance of 9 meters. In a mature stand large trees were more regularly spaced than
129 random (Wells & Getis 1999); density-dependent competition that leads to stand thinning is a
130 possible explanation for the observed pattern in adults.

131   It is estimated that *P. torreyana* reaches sexual maturity at around 10 to 20 years (Lanner
132 1998). The oldest tree found in the McMaster (1980) study was 125 years old. A dendro-
133 climatological study aged two of the largest, cone bearing trees from the reserve to
134 approximately 190-200 years old (Biondi et al. 1997).

135   Torrey pine seeds are heavy and protected with a thick hull and vestigial wings, making
136 wind dispersal highly unlikely; 50% of seeds fall or are removed by animals from the cone in the
137 first four months (Johnson et al. 2003). While McMaster (1980) proposed that seeds removed by
138 predators are lost from the seed bank, Johnson et al. (2003) argued that forgotten animal caches
139 are an important mechanism for seedling recruitment and longer distance seed dispersal, as has
140 been observed in the closely-related *P. coulteri* (Borchert et al. 2003).

141

142 Data Collection

143 In order to field map the entire population of *P. torreyana* at TPSR, first, visual identification of
144 tree canopy on color orthoimages (USGS 2004, 3 m resolution) was used to locate areas of *P.*
145 *torreyana* trees within TPSR. This was followed by a systematic search conducted over a period
146 of several months from May to October 2006. All individuals were mapped with a Trimble Geo
147 XM 2003 global positioning system (GPS) receiver (Trimble Navigation, Sunnyvale, CA, USA)
148 with 1-3 m accuracy using real time differential correction and post-processing to improve
149 spatial accuracy. The location of inaccessible trees (approximately 10 percent) was estimated
150 using Impulse 200 laser rangefinder (Laser Technology Inc., Centennial, CO, USA) to measure
151 distance and slope from the recording location, and a compass to measure the azimuth. The
152 geographic offset feature on the GPS used this information to calculate the tree location from the
153 recording location. For these inaccessible trees, measurements such as DBH and height were
154 visually estimated.

155   The following stages classes were defined for the purposes of this study: adult (trees
156 taller than 160 cm with cones); sub-adult (> 160 cm without cones); saplings (30 - 160 cm tall),
157 and seedlings (< 30 cm tall). For each adult and sub-adult tree we measured diameter at breast
158 height (DBH) at 1.3 m height on the trunk, and recorded presence of cones. For saplings and
159 seedlings we also measured height from the base to shoot apex (Thompson 1985), and for all
160 seedlings we counted number of branch whorls (which tends to be correlated with age in young
161 *P. torreyana*).

162   Each seedling located in 2006 was revisited approximately one year later in the
163 subsequent dry season, Sep-Dec 2007, in order to record survival and to search for additional
164 seedlings. *P. torreyana* seedlings are rare, difficult to spot, and appear to recruit in a clustered
165 pattern. Therefore, we conducted an additional adaptive sampling survey (Thompson 1992) of
166 forty random 10 x 10 m plots in 2006 whose locations were stratified by adult density. However,
167 there were no seedlings found in any of these plots.

168

169   Population Structure

170   Population size and structure were first characterized for the TPSR population as a whole.
171   Population structure, the frequency distribution of individuals by age, may reveal patterns of
172   historical recruitment and mortality in a long-lived species. However, because we could not core
173   all the individuals of this protected species using an increment borer in order to count annual
174   growth rings, we used size (DBH) as a surrogate for age in this study, given that a correlation
175   was previously established for TPSR (Wells & Getis 1999). Although this strategy is often used
176   for conifers (Newton 2007), the results must be interpreted with caution, as variable growth rates
177   of individuals can lead to flawed conclusions regarding population dynamics when size is used
178   as a surrogate for age (Keith 2000).

179   Population size structure was also characterized for subpopulations in order to describe
180   geographical variation in stand structure. TPSR was stratified into subregions based on spatial
181   clustering of the mapped trees themselves. Spatial pattern analysis methods, including those
182   used in this study, assume stationarity (Baddeley et al. 2005). A stationary point pattern has
183   homogenous density and variance in all parts of the study area and in all directions (Fortin &
184   Dale 2005). Within a study area, a variety of ecological processes act on different spatial and
185   temporal scales resulting in nonstationarity of tree density. The tree map was divided into
186   subregions that could meet the assumption of stationarity. A simple spatial clustering technique
187   was used to identify groups of more than 50 trees in which every tree was no further than 35
188   meters from another tree in the cluster. This lag distance of 35 meters was chosen as the best
189   compromise of tree density homogeneity within a group, reasonable number of tree groups, and
190   maximum number of trees included. This clustering method is similar to other local density
191   methods used to detect homogenous subplots described by Pélissier & Goreaud (2001).

192   Some resulting tree clusters were further subdivided into areas of uniform aspect and
193   slope. Size distribution was characterized and point pattern analyses conducted separately for
194   each of the spatial clusters, referred to as tree stands in the remainder of this paper. Stands less
195   than 2 ha were excluded from spatial analysis because of the large potential for edge effects with
196   an irregular boundary. This resulted in 15 stands with adequate numbers of trees for spatial
197   analysis and included 80% of all trees.

198

199   Point Pattern Analysis of Tree Spatial Pattern

200   A frequently observed pattern in forests is for young trees to be spatially clustered and mature
201   trees to be more evenly dispersed, suggesting density dependent mortality during stand
202   development (McDonald et al. 2003). Point pattern analysis was used in this study to identify
203   spatial patterns that suggest historical stand development processes such as density dependence,
204   competition, dispersal limitations, and episodic, patchy recruitment (Franklin in press). Multiple
205   point pattern analysis techniques were used in tandem (Perry et al. 2006). These included
206   univariate and bivariate versions of global tests, and a local test, in order to explore within group
207   and between group spatial patterns for adult and juvenile trees.

208   Global spatial statistics were calculated separately for each stand of trees using the ADS
209   software package in the R statistical environment (R Development Core Team, 2007). First we
210   examined univariate patterns for all trees and for mature trees (adults and sub-adults), and
211   juvenile trees (seedlings and saplings) separately. These global statistics determine if events

212 (tree locations) differ from a pattern of complete spatial randomness (CSR) (Perry et al. 2006).
213 Ripley's K (Ripley 1981) was used to identify clustering or over-dispersion (a regular pattern) of
214 points at a range of distances (Fortin & Dale 2005; Ripley 1981) and allowed our results to be
215 compared with Wells & Getis (1999). The neighborhood density function (NDF), a non-
216 cumulative annular variation of Ripley's K, prevents extreme values indicating clustering at
217 shorter lag distances from influencing the values calculated at longer lag distances (Condit et al.
218 2000). As a consequence, NDF can provide detail at a finer scale for specific lag distances;
219 however, it is also more sensitive to noise as a result of small sample size (Perry et al. 2006).
220 We considered spatial lags ranging from 1 to 35 m in 1-m increments. Edge effects were
221 addressed using ADS's correction method for complex sampling widows proposed by Goreaud
222 & Pélissier (2001). The observed patterns were compared to a null hypothesis of CSR at each lag
223 distance using 500 Monte Carlo simulations to create a confidence envelope, $\alpha = 0.01$.

224 We next evaluated the spatial relationship between adult and juvenile trees using
225 bivariate versions of Ripley's K and the NDF using the same parameters for range, lag distance,
226 and edge correction as the univariate global analyses. These bivariate methods look for
227 clustering (attraction) or dispersion (repulsion) between two types of events at specific lag
228 distances (Fortin & Dale 2005). The bivariate patterns were evaluated under a null hypothesis of
229 population independence which assumes that the locations of points in each group are
230 independent of the other, that there is no relationship between the locations of adult and juvenile
231 trees (Goreaud & Pelissier 2003). Attraction would be expected if dispersal limitation was the
232 dominant process, and repulsion if density dependent mortality affected juveniles near adults.
233 The null hypothesis of spatial independence was again tested with 500 Monte Carlo simulations
234 to create confidence limits of $\alpha = 0.01$ using a technique in which the spatial pattern of each
235 population is shifted by random toroidal vectors.

236 A local spatial statistic, Gi^* (Ord & Getis 1995), allowed us to examine the size of trees
237 around each individual tree up to a critical distance to determine if the observed size of
238 neighboring trees is larger or smaller than expected by random chance, thus identifying clusters
239 of small or large trees that might result from patchy recruitment or environmental conditions.
240 Following Wells & Getis (1999), the critical distance was defined as the lag distance at which
241 the rate of change for spatial clustering derived from the Ripley's K statistic becomes equal to or
242 less than the rate of change in clustering for an expected pattern for CSR, determined from the 15
243 stands in the global analyses. The output of the Gi^* analysis is a standardized z-score for each
244 tree point which identifies the magnitude of deviation from expected. By setting a 99%
245 confidence limit, the tree points with z-score > 2.58 are identified as members of a cluster of
246 large trees and tree points with a z score < -2.58 as members of a cluster of small trees (ESRI
247 1992).

248

249 Factors affection seedling recruitment and survival

250 We expected seedling recruitment to be influenced by available soil moisture and light
251 competition, as well as herbivory. Both seedling occurrence and seedling survival were analyzed
252 in relation to the following environmental variables derived from digital maps in the GIS:
253 vegetation community, soil type, slope aspect and slope angle derived from a digital elevation
254 model, distance from coast, and distance from nearest adult. Percent cover of litter was
255 measured in the field and tested as a predictor. Absence observations for the seedling occurrence

256 model consisted of 100 random point locations throughout the study area, positioned at least 50
257 meters from any known seedling, and these locations were visited in the field to confirm seedling
258 absence.

259   Because the response variables are binomial (seedling survival, or seedling presence/
260 absence), multiple logistic regressions were used to evaluate the relationship of these response
261 variables with environmental factors (McCabe & Moore 2006). A stepwise approach was used
262 to examine the relationship of each predictor with each response. The strongest single predictors
263 for each response variable (fir with simple models) were examined in two-predictor models,
264 followed by combining the strongest two-predictor models in multiple predictor combinations.
265 The statistical significance and fit of the models were evaluated with the Pearson χ^2 statistic
266 (Quinn & Keough 2002). Further, both the Akaike information criterion (AIC) and Bayesian
267 information criterion (BIC) were used to select the most parsimonious multi-predictor model.
268 While both of these likelihood-based criteria summarize a model by taking into account sample
269 size and number of predictors, BIC more harshly penalizes increased model complexity (Quinn
270 & Keough 2002). Logistic regressions were estimated using Systat 12 (Systat, Chicago, IL,
271 USA).

272

273 **Results**

274 Population Structure

275 A total of 5422 trees were mapped and measured at TPSR including 3805 trees classified as
276 adults, 888 sub-adults, 462 saplings and 267 seedlings (Table 1). The DBH size distribution for
277 all trees shows a strongly right-skewed pattern dominated by trees in smaller size classes (Figure
278 1). The height distribution for all trees less than 2 m tall (Figure 2) shows a spike for trees less
279 than 20 cm and a uniform height distribution for tress measuring between 20 cm and 200 cm.

280   Tree size structure varied throughout the reserve. TPSR is divided into two sections, the
281 Main Reserve (515 ha) and Extension (75 ha). Of the 15 stands identified by spatial clustering,
282 the "Main Stand" (located within the Main Reserve) is unique due to its large size (33 ha),
283 encompassing 27% (1441) of all trees recorded at TPSR. The other stands range in area from
284 1.5-7.0 ha and density ranged from 27 to 135 trees per ha with a median value of 45.4 (Table 1).
285 All but one stand at the Main Reserve has a right skewed size distribution with a much larger
286 representation of trees in the smaller size classes; the exception, "Main Flat Plateau" has a
287 uniform tree size distribution (Figure 3). On the other hand, stands in Extension showed a more
288 uniform tree size distribution, particularly for trees up to 40 cm DBH (see Online Resource 1,
289 Figure OR.1)

290

291 Tree Spatial Pattern

292 The predominant pattern detected with global Ripley's K for all trees within stands of greater
293 than 150 trees was that of clustering at all lag distances investigated when compared to CSR.
294 Because mature trees (adults plus sub-adults) constituted 87% of all trees, Ripley' K calculated
295 for mature trees was again predominated by clustering at all lag distances and so only the results
296 for mature trees are shown (Figure 4). Stands with fewer trees were more likely to exhibit small
297 lag distances without clustering. Ripley's K for juvenile trees, which was calculated for the eight
298 stands with greater than 20 juveniles, also showed a predominant pattern of clustering across all

lag distances when compared to CSR (Figure 5). As with Ripley's K, NDF for all trees and mature trees shows clustering across lag distances for the stands with the most trees. However, stands with fewer than 200 trees were increasingly likely to show a tree pattern that does not differ significantly from expected CSR at spatial lags < 10 m (Figure 4). "Parry Grove" stands out as the only stand with an over-dispersed tree pattern for lag distances between 21 and 31 m for all trees and mature trees (Figure 4). Also similar to Ripley's K, NDF indicates clustering across most lag distances < 10 m for juvenile trees, especially in the stands with the most juveniles, while most stands show tree patterns of both clustering and CSR at lag distances > 10 m (Figure 5).

Bivariate Ripley's K and NDF were calculated for the eight stands with more than 20 juvenile trees. Five of these stands did not show any significant pattern of attraction or repulsion between adult and juvenile trees, while three showed some degree of attraction between adult and juvenile trees for both Ripley's K and NDF at lag distances less than 15 m (Figure 6). The Getis-Ord Gi* statistic was mapped and showed that groups of trees with smaller than average DBH tended to be located in stands on the outside edges of the reserve and groups of trees with larger than average DBH to be located within the center of the reserve (shown for the Main Reserve in Figure 7; and for the Extension in Online Resources 1, Figure OR.2). In one edge stand (Parry Grove), clusters of small trees apparently resulted from tree planting following the bark beetle outbreak in the 1980s (Figure 7).

Seedling Recruitment and Survival

A total of 234 seedlings were located during the first field season (2006), and an additional 33 seedlings were located in late fall 2007. It is important to keep in mind that "seedlings" in this study include individuals up to 30 cm tall and so are not restricted to first-year recruits. In fact, 49% of seedlings had 1-10 whorls, suggesting that they were at least 1-10 years old. Survival from fall 2006 to fall 2007 averaged 62% and ranged from 0% to 82.8% by stand. Growth in height for surviving seedlings averaged 2-3 cm (details in Santos 2009). The occurrence (presence/absence) of seedlings was negatively related to distance from adult, positively related to slope steepness and southwesterly aspect, and was also related to soil class (Table 2a). This best multiple predictor model only included distance to adult and soil class and explained 43% of the variability in seedling occurrence. The odds of seedling presence were higher on 'Terrace Escarpments' than other soil classes (Online Resource 1, Figure OR.3).

Chances of seedling survival increased with seedling height and percent cover of ground litter and was also related to vegetation and soil class (Table 2b). Two vegetation classes, 'Torrey Pine/ Southern Maritime Chaparral' with decreased seedling survival, and 'Torrey Pine Woodland' with increased seedling survival, were the driving vegetation predictors for the model (Online Resource 1, Figure OR.4). However, this model only accounts for 10% of the variability in seedling survival.

Discussion

Earlier expert estimates putting the *P. torreyana* population at TPSR of 6000-7000 were fairly close to our census count of 5422 trees. However, the discovery of more than a thousand seedlings, saplings and sub-adult trees was somewhat unexpected. Earlier studies that sampled

342 small areas of TPSR reported little to no natural seedling recruitment in the absence of fire as a
343 canopy-opening disturbance (McMaster 1980, Wells & Getis 1999). As a result, we expected to
344 find a population structure dominated by older individuals in the larger size classes. Instead, we
345 found the size distribution to be dominated by trees in the smaller size classes in a "reverse J-
346 shaped" distribution which is suggestive of a population that is recruiting in sufficient numbers
347 to maintain itself (Harper 1977).

348   However, stand structure is variable across TPSR. While the right-skewed size
349 distribution is observed across all but one stand in the Main Reserve, the tree size structure of
350 most stands in the Extension is either uniform, or peaks at larger tree sizes. This implies that
351 conditions throughout the Extension may have been less conducive to recruitment in recent
352 decades, especially in some stands where the tree size distribution peaks at 35-60 cm DBH.

353   It should again be emphasized that this assessment of the population is based on size, not
354 age. While size is correlated with age in Torrey pines (Wells & Getis 1999), there is great
355 variability in size regardless of age owing to size plasticity in response to different growing
356 conditions (Knowles & Grant 1983). For example, *P. torreyana* growing on wind-blown, ocean-
357 facing cliff faces can remain short throughout their lives and the largest trees only grow in moist
358 well protected areas. As a result, the variation in tree size structure across the reserve is
359 indicative of both disturbance history and site conditions which have ongoing effects on
360 recruitment and tree growth.

361   We expected the overall spatial pattern of trees to follow the previously described pattern
362 of clustering in juvenile stages and over-dispersal (more uniform than random) for larger more
363 mature trees (Wells & Getis 1999). For juvenile *P. torreyana*, Ripley's K did show a
364 predominate pattern of clustering at all distances, and clustering at a variety of distances with
365 NDF, with no evidence of over-dispersion. This pattern in young trees is often the result of
366 dispersal limitations, or the patchy distribution of suitable micro-habitat that favor recruitment
367 and survival in certain areas over others (Palmiotto et al. 2004). The clustered pattern across
368 most lag distances for *P. torreyana* juveniles suggests a patchy distribution of establishment
369 and/or survival at a range of scales, yet does not unequivocally point to a specific mechanism
370 driving this recruitment pattern.

371   Unexpectedly, Ripley's K also showed a pattern predominated by clustering with no
372 evidence of over-dispersion for mature trees. In literature, mature trees typically show patterns
373 of over-dispersion, especially at shorter lag distances, owing to self thinning resulting from
374 competition for resources including light, space, moisture, and nutrients (Kenkel 1988;
375 McDonald et al. 2003). While tree patterns in one third of the stands were not significantly
376 different from CSR at lag distances less than 5 m, all other stands showed clustering at these
377 short distances. This suggests that the clustered patterns resulting from patchy recruitment and
378 survival of juveniles persist over time and that density dependent thinning may not be an
379 important process for this population. Our mature tree category includes a range of tree sizes
380 with DBH ranging from 2 to 136 cm. It is possible that we were not seeing a pattern of over
381 dispersion in some stands because some of the trees included in the analysis are too small to
382 show effects of density dependent thinning. To test this, we re-did re the Ripley's K and NDF
383 analyses for all trees with a DBH greater than 20 cm and the predominant pattern of clustering
384 was again observed across all stands (details not shown).

385   Bivariate point pattern analysis did not indicate any particular attraction or repulsion
386 between juvenile and mature trees at most lag distances in most stands. This suggests that
387 density dependent mortality, where small trees found near large trees are more likely to die, is
388 not an important process in this population. Alternatively, there may initially be very high
389 numbers of juveniles near adults, owing to dispersal limitations, and subsequent (unobserved)
390 density-dependent mortality could have lead to the observed pattern.

391   In the local spatial analysis, we expected to find local clusters of smaller than and larger
392 than average trees based on patchiness of environmental conditions and different disturbance
393 histories throughout the reserve. This was supported by the Getis-Ord Gi* statistic that
394 identified numerous clusters of smaller than average trees particularly along the edges of the
395 reserve and clusters of larger than average trees well within reserve boundaries. This suggests
396 that along the reserve edges there may be conditions that enhance recruitment of new trees, such
397 as proximity to urban development and therefore supplemental water (especially in the
398 Extension), or, more open understory along the coastal bluffs. Conversely, conditions (such as a
399 dense shrub cover) within the central areas may inhibit recruitment or seedling survival.

400   These clusters of smaller than average trees indicate where in TPSR trees have recruited
401 in large numbers in recent decades. In contrast, some stands or portions of stands show clusters
402 of larger than average trees indicating locations that lack successful recent recruitment. In a
403 population of trees, it is not expected for individual trees to establish and survive uniformly in
404 time or space. However, this description of local pattern with respect to size indicates locations
405 of episodic recruitment and/or differential survival, and may assist managers in prioritizing areas
406 to monitor the population, or in deciding where to conduct restoration projects.

407   We expected to find little or no recruitment based on earlier studies. Instead, we
408 documented 260 trees less than 30 cm tall, concentrated in a few stands but found across varied
409 habitats and even in areas with significant human disturbance. Their spatially clustered
410 distribution is additional evidence that a patch generating process, such as dispersal limitations or
411 patchy environmental conditions, is acting on recruitment and survival.

412   Given that this pine species is a poor disperser, sensitive to dry conditions at the seedling
413 stage and a poor competitor (shade intolerant), we expected seedlings to be positively associated
414 with adult trees and absent from dense, shrubby vegetation and xeric habitat conditions. While
415 we did find the expected relationships between seedling presence and proximity to adult trees,
416 vegetation type and soil type, there was not a strong relationship with slope or aspect which are
417 typically used as surrogates for topographic moisture conditions (Moore et al. 1991). The
418 apparent preference for "Terrace Escarpments" may be the result of reduced competition with
419 other vegetation as few plants survive on this open sandy soil.

420   The overall "seedling" survival rate of 62% from 2006 to 2007 was unexpected as earlier
421 studies had reported survival rates of less that half that, but instead of describing first-year
422 survival rate, our data included a number of age cohorts. We also anticipated low seedling
423 survival on more xeric sites and in denser vegetation. The significant relationships with
424 vegetation class and litter cover (positive) suggest that these factors may be acting as surrogates
425 for moisture availability. Litter may act as mulch, inhibiting soil water loss through evaporation,
426 and vegetation types associated with higher seedling survival, such as "Torrey Pine Woodland,"
427 may provide some soil shading but lack dense understory vegetation that competes with
428 seedlings for soil moisture. However, only 10% of the variability in seedling survival was

429 explained by these variables. Seedling survival may highly stochastic but also the mapped
430 environmental predictors used may not have described site conditions at a fine enough scale to
431 explain seedling survival.

432

433 **Conclusion**

434 This study demonstrates the feasibility of collecting comprehensive data for populations of long
435 lived, rare plants that can provide important insights for monitoring and management. This is
436 especially critical for populations that occur over varied terrain where patterns of recruitment,
437 growth, and survival vary in space and time. The census also provided a large and complete
438 dataset necessary for the spatial analyses. These analyses provide insights that link the patterns
439 of observed trees and seedlings to the ecological processes that might control them. The high
440 degree of clustering and varied stand densities further emphasize the different processes or
441 disturbance histories acting across the populations. For example, Lover's Lane, the stand with
442 the highest density and a large proportion of smaller trees, occurs on a former construction site;
443 also the tree pattern at Parry Grove resulting from a planting effort following the bark beetle
444 outbreak was captured by the spatial analysis. Our study suggests that recent human
445 intervention, accidental or purposeful, is an important driver of population change for *P.*
446 *torreyana*.

447   This dataset provided information that can guide the allocation of resources such as
448 where to monitor seedling recruitment and adult survival. It also allows a greater focus on other
449 reserve species since there is no current evidence of decline in the focal species, *P. torreyana*. In
450 addition, the dataset provides a baseline for continued monitoring. In 50 or 100 years, these data
451 may be far more useful than they are now.

452

458

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555

Table 1. Number of *P. torreyana* for each size class in 15 stands (defined by spatial clustering of tree stem map), tree density, average DBH and stand area. "Other trees" are those outside the stands identified by spatial clustering in the Main Reserve (490 ha) and Extension (80 ha) of Torrey Pines State Reserve.

Stand	Adult	Sub-Adult	Sapling	Seedling	Total Trees	Area (ha)	Tree density (/ha)	Average DBH (cm)
Main Reserve	**2400**	**667**	**345**	**191**	**3603**	--	--	--
Main Stand	1072	251	88	30	1441	32.72	44.04	28.14
East Grove	351	83	13	3	450	7.00	64.31	22.34
Lover's Lane	232	74	61	35	402	2.98	135.10	17.80
West Guy Fleming	129	64	55	81	329	3.45	95.48	12.19
Broken Hill Trail	87	30	15	6	138	2.45	56.21	18.95
Parry Grove	29	61	35	0	125	2.10	59.62	5.72
Razor Point	60	15	12	1	88	2.00	44.01	12.59
Main Flat Plateau	46	5	0	0	51	1.77	28.79	35.09
Other trees	394	84	66	35	579	--	--	24.21
Extension	**1405**	**221**	**117**	**76**	**1819**	--	--	--
West Extension	360	41	19	4	424	5.74	73.85	28.20
East of Red Top	217	86	48	6	357	4.88	73.15	16.05
Red Top	119	10	4	0	133	3.42	38.91	25.41
South of Red Top	57	14	7	45	123	1.45	84.96	14.73
Ext. Center Ridge	116	2	4	0	122	3.24	37.71	37.90
Ext. West Ridge	94	4	1	0	99	2.69	36.75	40.23
North Extension	69	20	0	0	89	3.36	26.50	33.52
Other trees	373	44	34	21	472	--	--	28.98
Total	**3805**	**888**	**462**	**267**	**5422**			

15

Table 2. Stepwise Logistic regression analysis for predicting seedling presence/absence. Results for significant single predictor models are shown, and best multiple predictor model as determined by lowest BIC and selected using stepwise procedures described in the text. The sign of the estimated coefficient is given for continuous and ordered predictors/

Models	Coefficient	χ^2	df	p	AIC	BIC	Rho^2
a) Seedling presence/absence							
Single Predictor Models							
Distance to Adult	Negative	124.93	1	<0.001	292.75	300.41	0.30
Soil Class	--	82.01	2	<0.001	337.67	349.16	0.20
Vegetation Class	--	94.18	5	<0.001	331.50	354.48	0.23
Slope (ordinal categories of steepness)	Positive	14.03	2	0.001	405.65	417.13	0.03
Aspect (ordinal categories; southwestness)	Positive	13.01	3	0.005	408.67	423.99	0.03
Best Multiple Predictor Model							
Distance to Adult + Soil Class		178.28	3	<0.001	243.40	258.72	0.43
b) Seedling Survival							
Single Predictor Models							
Height	Positive	11.53	1	0.001	327.97	335.06	0.03
% Ground Litter	Positive	8.73	1	0.003	330.78	337.87	0.03
Soil Class	--	11.79	2	0.003	329.71	340.35	0.04
Vegetation Class	--	16.90	5	0.005	321.26	342.29	0.05
Best Multiple Predictor Model							
Height + % Ground Litter + Vegetation Class + Soil		31.25	9	<0.001	314.99	350.05	0.10

Figure 1. Frequency distribution of tree diameter at height of 1.3 m for all trees at TPSR.
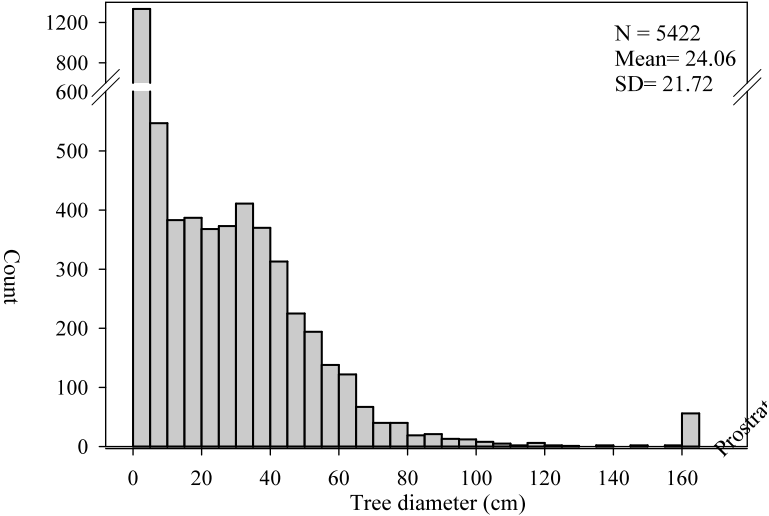
Figure 2. Frequency distribution by height for all trees at TPSR with a height of less than 200 cm
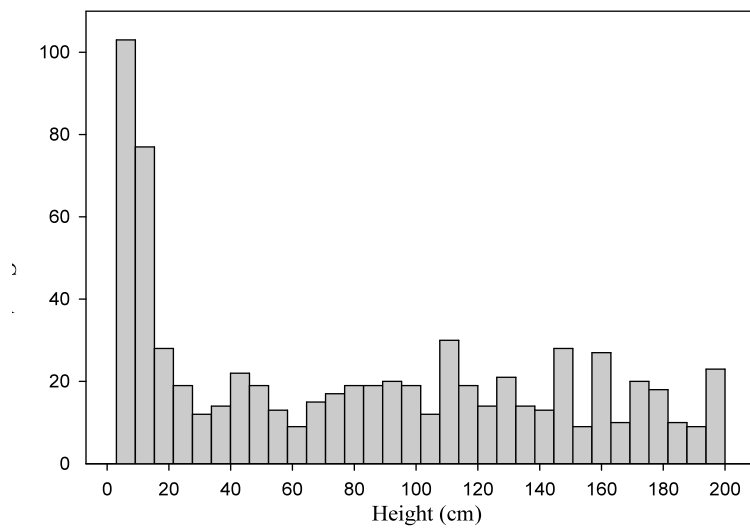
Figure 3. Frequency distribution of tree diameter for each stand in the Main Reserve section of the Torrey Pines State Reserve (Table 1).
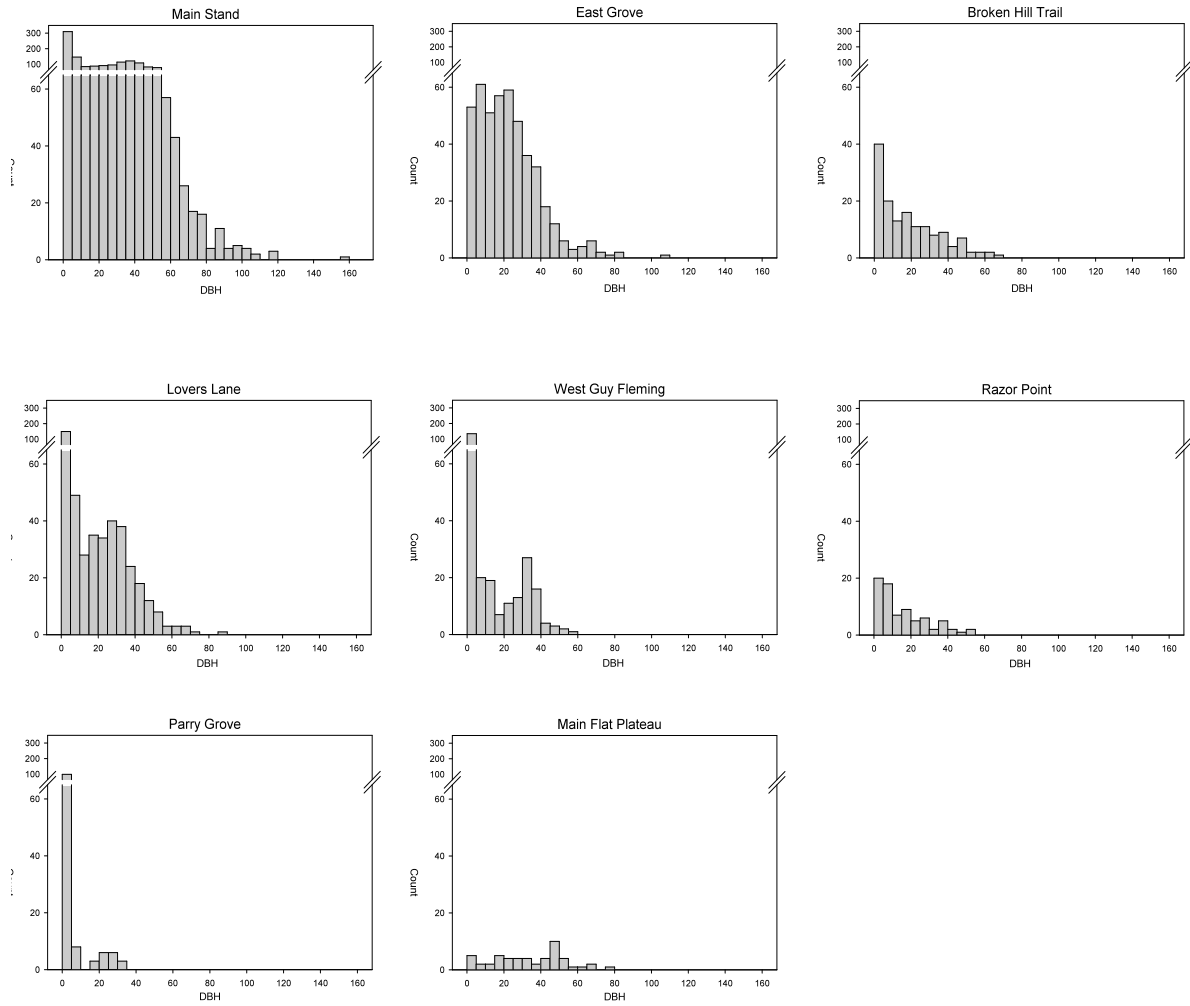
Figure 4. Comparison of univariate Ripley's K function and NDF calculated on all mature (adult and sub-adult) trees within stands. Gray shading indicates the point pattern does not differ from CSR at that lag distance, black shading indicates clustering and white areas indicate an over-dispersed point pattern at a given lag distance (1-35 m).

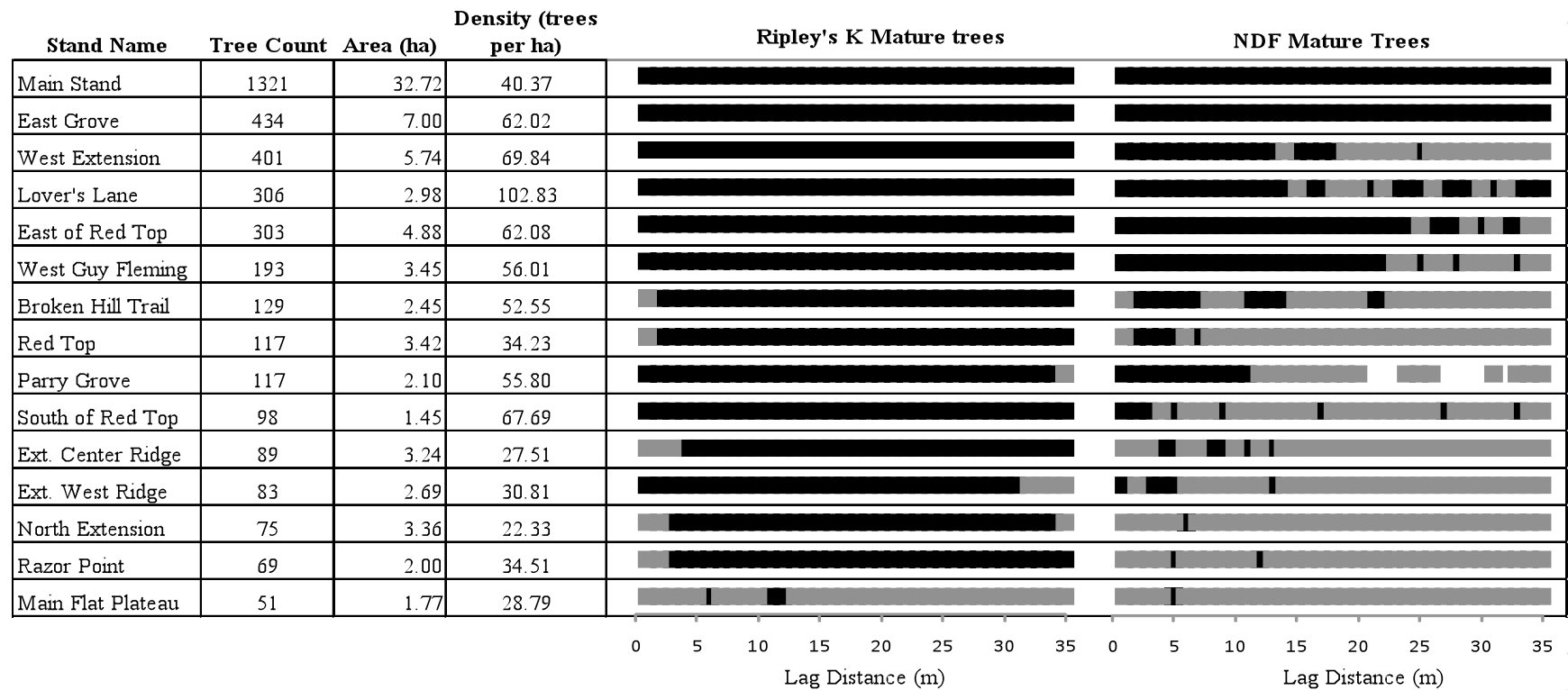| Stand Name	Tree Count	Area (ha)	Density (trees per ha)	Ripley's K Mature trees	NDF Mature Trees
Main Stand	1321	32.72	40.37		
East Grove	434	7.00	62.02		
West Extension	401	5.74	69.84		
Lover's Lane	306	2.98	102.83		
East of Red Top	303	4.88	62.08		
West Guy Fleming	193	3.45	56.01		
Broken Hill Trail	129	2.45	52.55		
Red Top	117	3.42	34.23		
Parry Grove	117	2.10	55.80		
South of Red Top	98	1.45	67.69		
Ext. Center Ridge	89	3.24	27.51		
Ext. West Ridge	83	2.69	30.81		
North Extension	75	3.36	22.33		
Razor Point	69	2.00	34.51		
Main Flat Plateau	51	1.77	28.79		

Lag Distance (m)   Lag Distance (m)

Figure 5. Univariate Ripley's K function and NDF calculated for juvenile trees for all stands with more than 20 juvenile trees. Gray areas indicate the point pattern does not differ from CSR, black areas indicate clustering at a given lag distance (1-35 m).

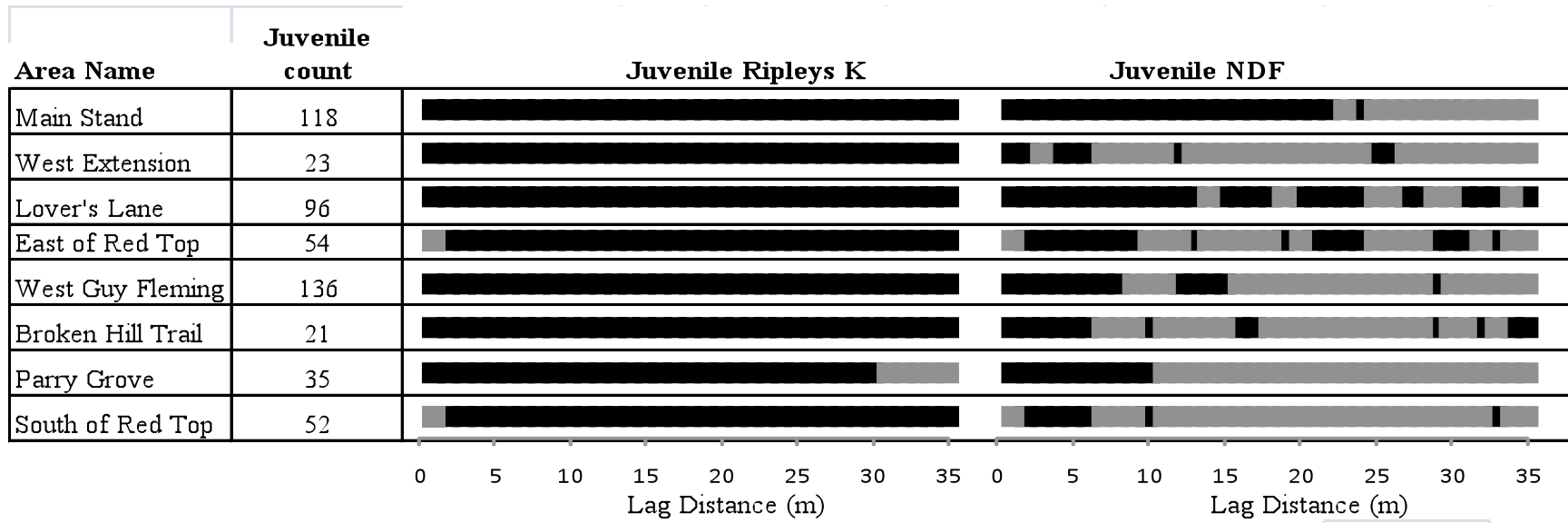| Area Name	Juvenile count	Juvenile Ripleys K	Juvenile NDF
Main Stand	118		
West Extension	23		
Lover's Lane	96		
East of Red Top	54		
West Guy Fleming	136		
Broken Hill Trail	21		
Parry Grove	35		
South of Red Top	52		

Lag Distance (m)   Lag Distance (m)

Figure 6. Bivariate Ripley's K function and NDF examining the spatial relationship between adult and juvenile trees across all stands with greater than 20 juvenile trees. Grey areas indicate the point pattern does not differ from CSR, black areas indicate attraction between adult and juvenile trees at a given lag distance (1-35 m).
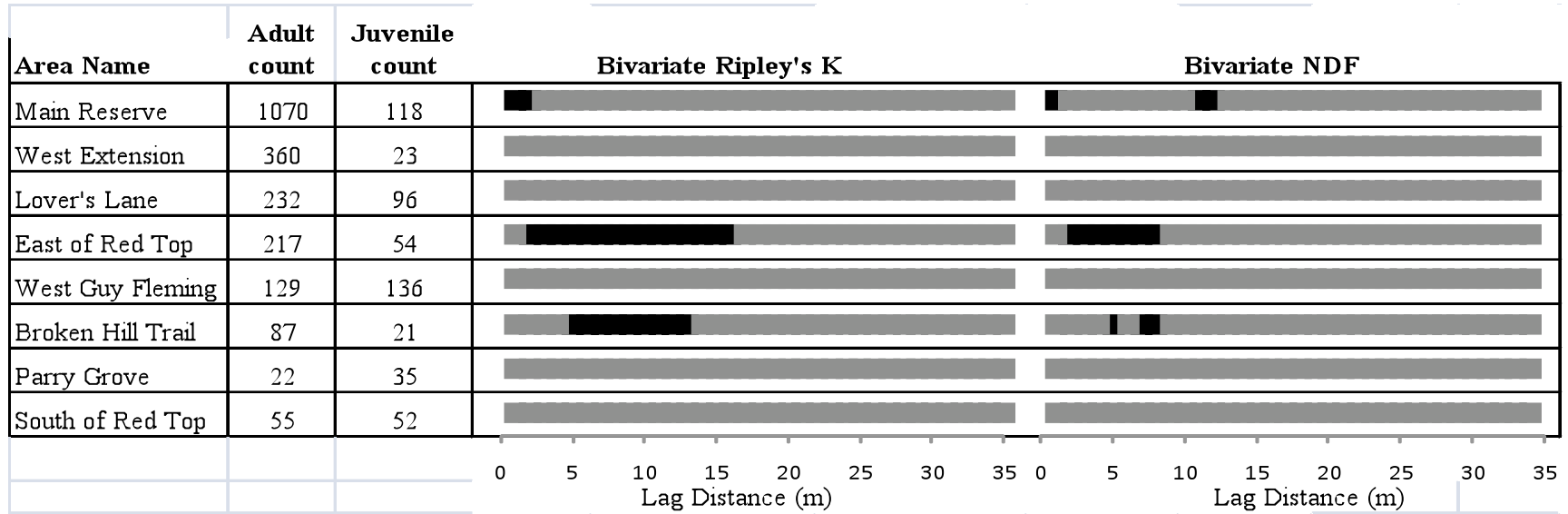
Area Name	Adult count	Juvenile count	Bivariate Ripley's K	Bivariate NDF
Main Reserve	1070	118		
West Extension	360	23		
Lover's Lane	232	96		
East of Red Top	217	54		
West Guy Fleming	129	136		
Broken Hill Trail	87	21		
Parry Grove	22	35		
South of Red Top	55	52		

Figure 7. The stands showing trees in the Main Reserve by size class (left), and trees for which Gi*was greater (member of a cluster of large trees) or less (member of a cluster of small trees) than expected (right).
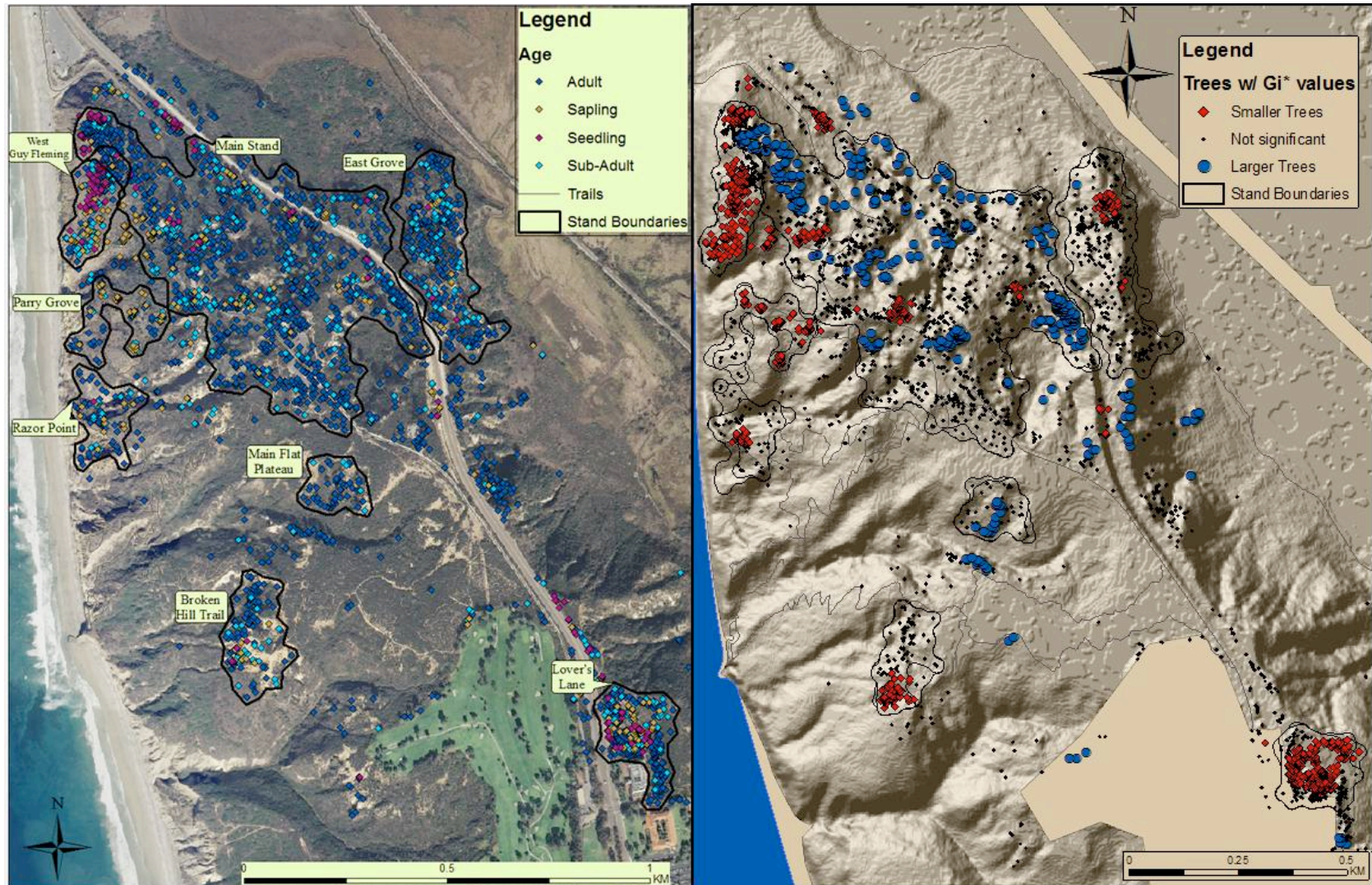
Online Resource 1

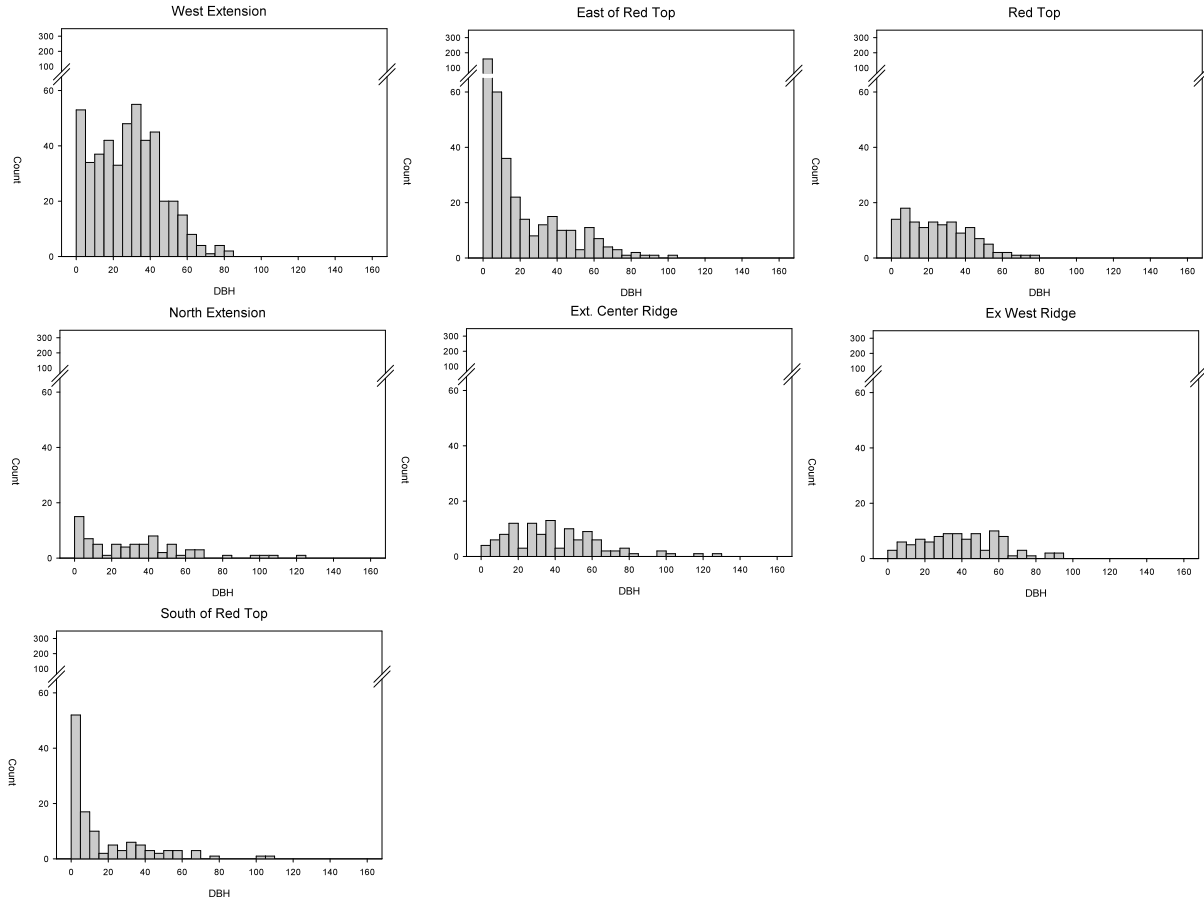Figure OR.1. Frequency distribution of tree diameter at 1.3 m height (DBH) for each stand in the reserve Extension.

Figure OR.2. The stands showing trees in the Extenstion by size class (top), and trees for which Gi*was greater (member of a cluster of large trees) or less (member of a cluster of small trees) than expected (bottom).
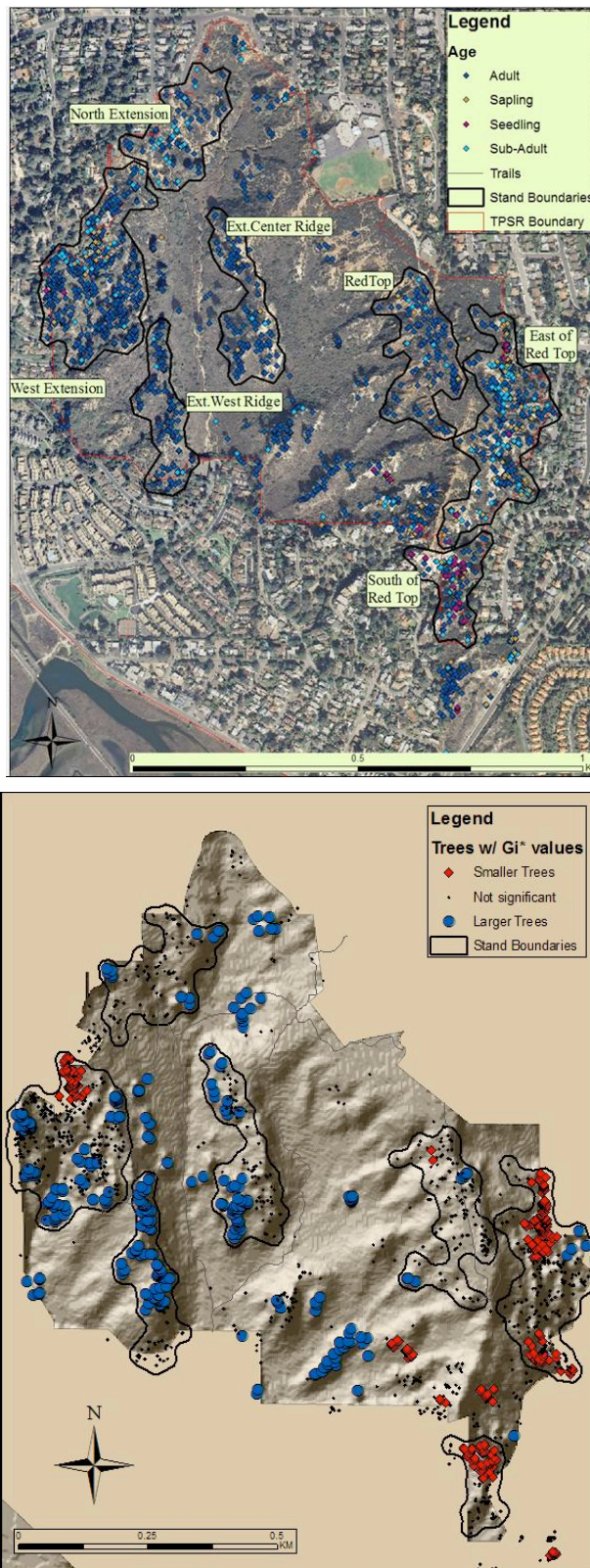
Figure OR.3. Odds Ratio of Seedling Presence against Soil Class (multiple predictor model).

Reference Group:
Soil Type: Loamy coarse + gravel sand
Presence Probability = 20.1%

Loamy alluvial + Loamy sand

Terrace Esc

amy coarsr
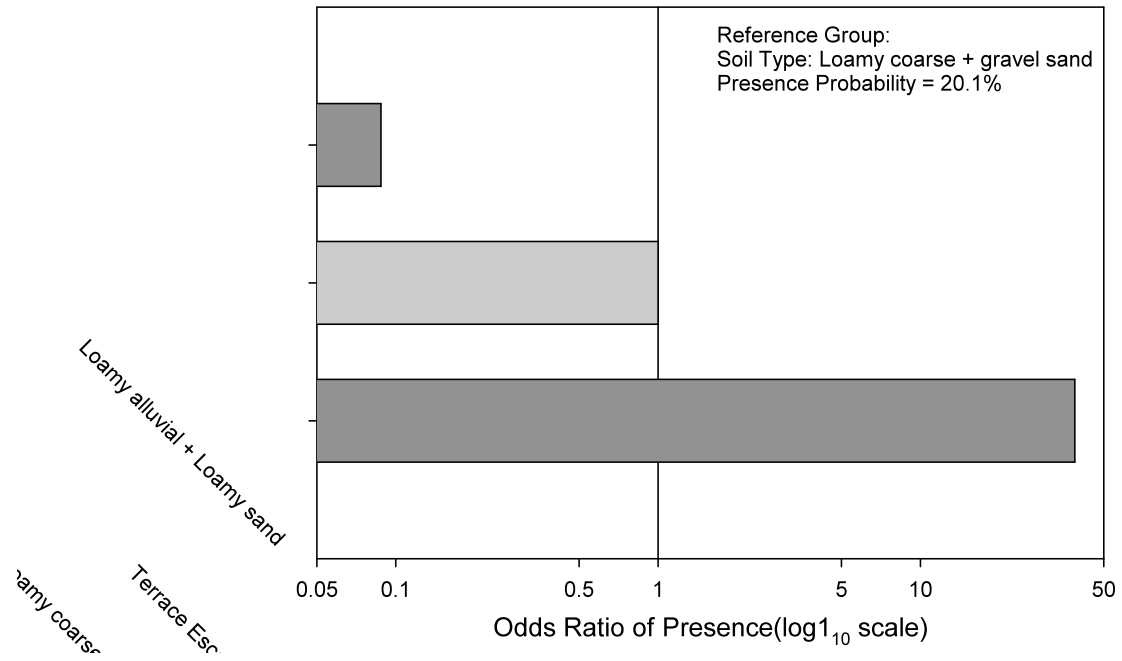
Odds Ratio of Presence(log1$_{10}$ scale)

Figure OR.4. Odds Ratio of Seedling Survival for vegetation class (multiple predictor model).

Reference Group:
Veg Class=Torrey Pines Forest
Survival Probability = 48.5%

TP / SM Chaparral

TP Forest

Bare ground/ urban

SM Chaparral - Herb

SM Chaparral - Shrub

TP Woodland

Odds Ratio of Survival (log$_{10}$ scale)