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Extreme Winter Storms Have Variable Effects on the Population Dynamics of Canopy Dominant Species in an Old-Growth Subtropical Forest

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Abstract: Extreme climatic events are predicted to increase in frequency and magnitude as global climate change continues. Extreme climatic events have profound impacts on community structure and dynamics, but their effects on the dominant species within a community remains unclear. To explore this issue, we analyzed changes in population dynamics and dead individuals' spatial pattern for several dominant species (*Castanopsis eyrei*, *Schima superba*, *Pinus massoniana*, and *Daphniphyllum oldhamii*) among different habitats in a subtropical forest before and after a significant winter storm that occurred in February 2008. Using the Gutianshan 24-ha forest plot as a representative sample, we found that the plot-level DBH of *P. massoniana* and *C. eyrei* significantly increased after the winter storm, while the plot-level basal area of *P. massoniana* and *S. superba* decreased significantly. In addition, *P. massoniana* was most affected by the storm (mortality: 9.08%; population change rate: −8.93%), followed by *C. eyrei* (mortality: 6.93%; population change rate: −4.91%). Small-diameter individuals experienced higher mortality rates, but the diameter structure of the dominant species at the population level remained basically stable. The number of individuals, the density of the dominant population, the number of mortalities, and the mortality rate of the dominant species differed among habitats. The spatial point patterns of the dead individuals at each life stage were mainly aggregated in distribution, and the degree of aggregation tended to decrease with increasing scale. In conclusion, the population dynamics of dominant species were significantly altered following the winter storm, but the extent of the changes varied with species. Our study suggests that analyzing the dominant species of a community contributes to a better understanding of the biological response of forest ecosystems in the face of extreme climatic events.

Keywords: subtropical evergreen broad-leaved forest; mortality rate; recruitment rate; diameter structure; spatial point pattern; forest dynamics plot

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1. Introduction

Ongoing global climate change increases environmental fluctuations and the frequency and intensity of extreme climate events (such as extreme winter storms and heat waves) [1,2]. Extreme climatic events, characterized as extremely rare, low frequency, and intense climatic events [3], have profound impacts on species composition, community dynamics, and local scale species interactions [4–6]. Winter storms are one of the main types of extreme

climate events, which can severely damage tree individuals in a community and cause branch breakage, stem snaps, tip ups, and even death [7–9]. The death or damage of these individual trees directly affects population characteristics and also changes the spatial pattern of species [9,10].

Canopy dominant species are an important part of the forest community, accounting for most individuals and most of the total biomass, and play a crucial role in forest structure and the formation of the forest environment [11,12]. Forest canopy species usually interact directly, through leaf area, with the external environment and are therefore subject to more stress and survival pressure [13,14]. Usually, when winter storms occur, large-diameter individuals in the canopy intercept large amounts of snow, resulting in extensive damage and sometimes death [15]. Therefore, canopy-dominant species reflect the extent of winter storm damage to the forest community. However, we still lack knowledge about how the population dynamics of canopy-dominant species respond differently in the face of extreme climate events.

Species could have strong habitat preference within a community due to their species characteristics and preferences for environmental factors such as nutrient and water availability, light availability, and topography [16,17]. The species distributed in habitats with high convexo-concave degree, slope, and elevation are more affected by winter storms [18]. Following winter storms, species often show different degrees of resistance due to species identity, tree diameter, and habitat differences, thus showing different mortality patterns [8,15,19–21]. Thus, the population dynamics of canopy-dominant species may show significant differences in different habitats following the winter storm.

The species spatial distribution pattern represents an arrangement of the individual-level structure within a community, and the degree to which individuals of species are aggregated or dispersed is crucial to understanding how a species uses environmental resources [22]. Previous study of spatial distribution patterns mostly focuses on the living individual to improve understanding of the mechanisms of species coexistence in diverse communities [23,24]. However, few studies focus on the species spatial pattern of individual dead trees following an extreme climate event such as a winter storm. Moreover, how winter storms influence the spatial pattern of dead individuals remains unknown. Therefore, considering the spatial patterns of individual dead trees caused by a winter storm could improve our understanding of the response of species to the winter storm in species-rich communities.

From 10 January to 6 February 2008, an extreme winter storm with ice and snow build-up in southern China caused massive mechanical damage to native subtropical forests [7,25]. China's State Forestry Administration (SFA) estimated that the storm damaged 20.86 million hectares, one tenth of China's forests and plantations [25]. The rare and extreme snow–ice storm was more damaging than the 1998 North American ice storm [7]. In the Gutianshan plot, the winter storm severely damaged one-third of trees, one-third were lightly damaged, and the remaining third were unaffected [8]. Heavy winter storms are extremely uncommon in Chinese subtropical forests, and the 2008 winter storm was the only storm observed in the region in the last fifty years [7]. To explore the effects of the winter storm on canopy dominant species populations in subtropical forests, we focused on the following questions by using the Gutianshan 24-ha forest plot as a representative sample:

(1) How do the population structures of the four canopy dominant species change following the winter storm?
(2) How does damage to the four canopy dominant species caused by the winter storm vary across habitat types?
(3) What is the spatial distribution pattern of dead individuals for the four dominant species?

2. Materials and Methods

2.1. Study Site and Tree Inventory

Qianjiangyuan National Park is located in the northwestern part of Kaihua County, Zhejiang Province, China. The national park encompasses a large, concentrated distribution

of low-altitude evergreen broad-leaved old-growth forests [26]. This unique zonal top community has nationally representative forest communities. This region is located in the central humid subtropical monsoon climate zone in China. The mean annual precipitation is 1964 mm and the mean annual temperature in this region is 15.3 °C [26]. The soil is mainly red soil, yellow-red soil, red-yellow soil, and mountain meadow soil [27]. The Gutianshan Nature Reserve in Qianjiangyuan National Park has about 57% natural forest, most of which is subtropical broad-leaved evergreen forest [28].

The study was carried out in the 24-ha old-growth subtropical forest dynamic Gutianshan plot in the Qianjiangyuan National Park in China (Figure 1). The 24-ha forest plot was established in October 2005 following the GTFS-ForestGEO protocol [29]. The elevation difference within the 24-ha plot of Gutianshan is 268.6 m, the highest elevation is 714.9 m, and the lowest elevation is 446.3 m. The slope in the plot was highly variable, ranging from 12.8° to 62° [28]. The whole 24-ha plot was classified into five habitat types: low valley; low ridge; mid-slope; high slope; and high ridge (Figure S1) [30]. The first tree census in the 24-ha forest plot was conducted in 2005, and all trees with diameter at breast height (DBH) ≥1 cm were mapped, measured (measure the DBH of trunk and branch), identified, and marked. According to that survey, there were 140,700 trees in total, with 159 species belonging to 49 families and 103 genera. The dominant species were *Castanopsis eyrei* (Champ. ex Benth.) Hutch., *Schima superba* Gardn. et Champ. and *Pinus massoniana* Lamb. [31].

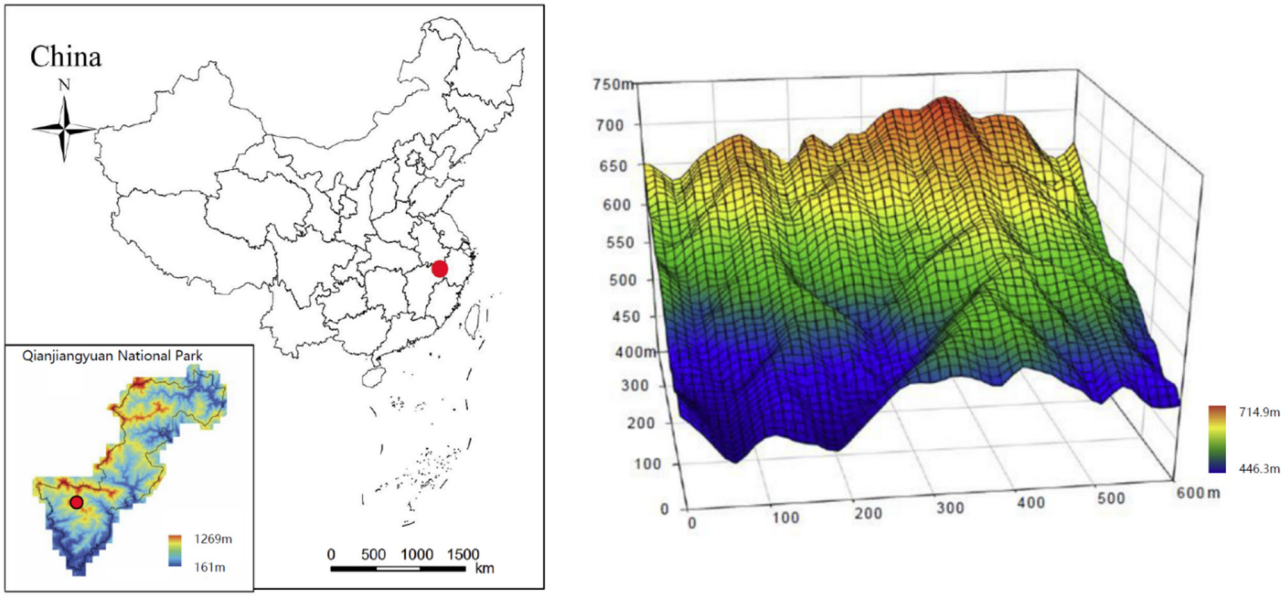


Figure 1. Location map of the 24-ha Gutianshan forest plot in Qianjiangyuan National Park in China. The red point signifies the study site. The axis in the 3D plot represents the height difference of the 24-ha plot.

2.2. Data Collection and Statistical Analysis

2.2.1. Importance Value of Dominant Tree Species

The importance value (IV) reflects the combined status and role of species in the community. IV was calculated as one-third of the sum of relative abundance (RA), relative frequency (RF), and relative dominance (RD) [32]. The formula is as follows:

$$IV = (RA + RF + RD)/3 \quad (1)$$

$$RA = n_i / \sum_{i=1}^{S} n_i \quad (2)$$

$$RF = f_i / \sum_{i=1}^{S} f_i \quad (3)$$

$$RD = d_i / \sum_{i=1}^{S} d_i \quad (4)$$

where n_i is the number of individuals of a certain population i; f_i is the number of quadrats in which the population i appears; d_i is the basal area at the height of 1.3 m of population i; and S is the total number of species. Based on IV values of species, four canopy dominant species were selected as focal species in the study, including three broad-leaf species and one conifer species: *C. eyrei*, *S. superba*, *P. massoniana*, and *Daphniphyllum oldhamii* (Hemsl.) K.Rosenthal.

2.2.2. Recruitment, Upgrade, and Mortality

Data from individual tree surveys from 2005 and 2010 for the four canopy dominant species were used to analyze the dynamics of recruitment, upgrading, and mortality. Recruitment individuals refers to newly emerged individuals with DBH $\geq$ 1 cm during the re-examination in 2010; dead individuals refers to the individuals that died or disappeared at the time of review; upgraded individuals refers to the individuals that left a certain diameter class due to growth [9]. We obtained the change rate of those populations over the five-year period by calculating the mortality rate and recruitment rate of different diameter classes of the dominant populations. Mortality rate and recruitment rate were calculated as:

$$\text{Mortality rate}: \ M = (lnN_0 - lnS_t)/T \quad (5)$$

$$\text{Recruitment rate}: \ R = (lnN_t - lnS_t)/T \quad (6)$$

where N_0 and N_t are the number of individuals of a population in the first and second surveys; S_t is the number of surviving individuals of population N_0 in the second survey; and T is the time interval between two surveys [33]. The population change rate is expressed as the difference between the recruitment rate and the mortality rate.

2.2.3. Diameter Structure Classes and Spatial Point Patterns

In order to explore how the spatial patterns of dead individuals caused by the winter storm for the four dominate species vary across different diameter classes, we first divide all the dead individuals into different diameter classes. According to the classification criteria of tree diameter class structure in subtropical evergreen broad-leaved forests [34], DBH size was classified into the following three categories to represent the different life stages (Figure S2): sapling (1 cm $\leq$ DBH < 5 cm); juvenile (5 cm $\leq$ DBH < 10 cm); and adult (DBH $\geq$ 10 cm).

The K-function proposed by Ripley [35] was used to describe the spatial point pattern of species:

$$K(r) = \left(\frac{A}{n^2}\right) \sum_{i=1}^{n} \sum_{j=1}^{n} \frac{1}{W_{ij}} \mathrm{Ir}(u_{ij}) (i \neq j) \quad (7)$$

where n is the number of individuals; u_{ij} is the distance between individuals i and j; r is the scale (if $u_{ij} \leq r$, $\mathrm{Ir}_{(u_{ij})} = 1$; if $u_{ij} > r$, $\mathrm{Ir}_{(u_{ij})} = 0$); W_{ij} is the boundary effect correction factor, which is the proportion of the circle with individuals i as the center and u_{ij} as the radius in area A; and A is the area. Converting Equation (7) yields:

$$L(r) = \sqrt{K(r)/\pi} - r \quad (8)$$

$L(r) = 0$ indicates that the population is randomly distributed; $L(r) > 0$ indicates that the population is aggregated; and $L(r) < 0$ indicates that the population is uniformly distributed. The $L(r)$ of the actual observed distribution deviates from the 95% envelope of the theoretical value. The confidence interval is obtained by the Monte Carlo method [36]. If $L(r)$ of the actual distribution falls within the envelope, the species is randomly distributed; if it is above the envelope, the species exhibits aggregated distribution; and if it is below the envelope, it is significantly uniformly distributed. We repeated this analysis simulation 999 times.

All analyses were conducted in the R 4.1.2 statistical platform [37]. Data grouping statistics were acquired using the *doBy* package [38]. We used a T-test to compare the differences in plot-level DBH and plot-level basal area from 2005 to 2010. The spatial point pattern was shown using the *spatstat* package [39] to calculate $K(r)$ and $L(r)$. The spatial point pattern of the four dominant species was shown using the *ggplot2* package [40].

3. Results

3.1. Changes in Population Characteristics of Canopy Dominant Species

The plot-level (20 × 20 m) DBH of *C. eyrei* and *P. massoniana* exhibited significant increases from 2005 to 2010, while the changes for *S. superba* and *D. oldhamii* were not significant (Table 1). For plot-level basal area, *S. superba* and *P. massoniana* significantly decreased from 2005 to 2010. However, the change in *C. eyrei* and *D. oldhamii* was not significant.

Table 1. Importance values, plot-level DBH, and plot-level basal area of the four canopy dominant species in 2005 and 2010.

Species	Importance Value		DBH (cm) at Plot Level †			Basal Area (m^2) at Plot Level †		
	2005	2010	2005	2010	*p*-Value	2005	2010	*p*-Value
Castanopsis eyrei	0.152	0.149	**14.495 (8.422)**	**16.292 (9.126)**	**0.001**	0.504 (0.365)	0.470 (0.353)	0.07
Schima superba	0.091	0.093	20.593 (9.862)	21.394 (10.253)	0.506	**0.283 (0.172)**	**0.268 (0.269)**	**0.04**
Pinus massoniana	0.048	0.042	**32.816 (13.741)**	**34.033 (12.818)**	**0.021**	**0.297 (0.218)**	**0.272 (0.199)**	**0.001**
Daphniphyllum oldhamii	0.022	0.023	6.853 (4.272)	7.201 (6.230)	0.191	0.036 (0.045)	0.034 (0.041)	0.445

† Mean (standard deviation) of DBH or Basal area at 20 m × 20 m plot level. Variables that *p*-value less than 0.05 are shown in bold-type.

The diameter structure of *C. eyrei* and *S. superba* showed bimodal distribution. Individuals of *C. eyrei* and *S. superba* mainly peaked at 2 cm and 30 cm (Figure 2a,c), while *D. oldhamii* showed multimodal distribution (Figure 2g). The *P. massoniana* population had a single peak structure to the right and tended to be aging and declining (Figure 2e). The numbers of recruitments, upgrades, and mortalities for *C. eyrei*, *S. superba*, and *D. oldhamii* populations all decreased with the increase in diameter classes (Figure 2b,d,h), while *P. massoniana* showed no significant decreasing trend in any category (Figure 2f). All the population change rates were negative (Table 2). The number of individuals in the small-diameter class (DBH 1–1.4 cm) decreased the most (Figure 2b,d,f,h).

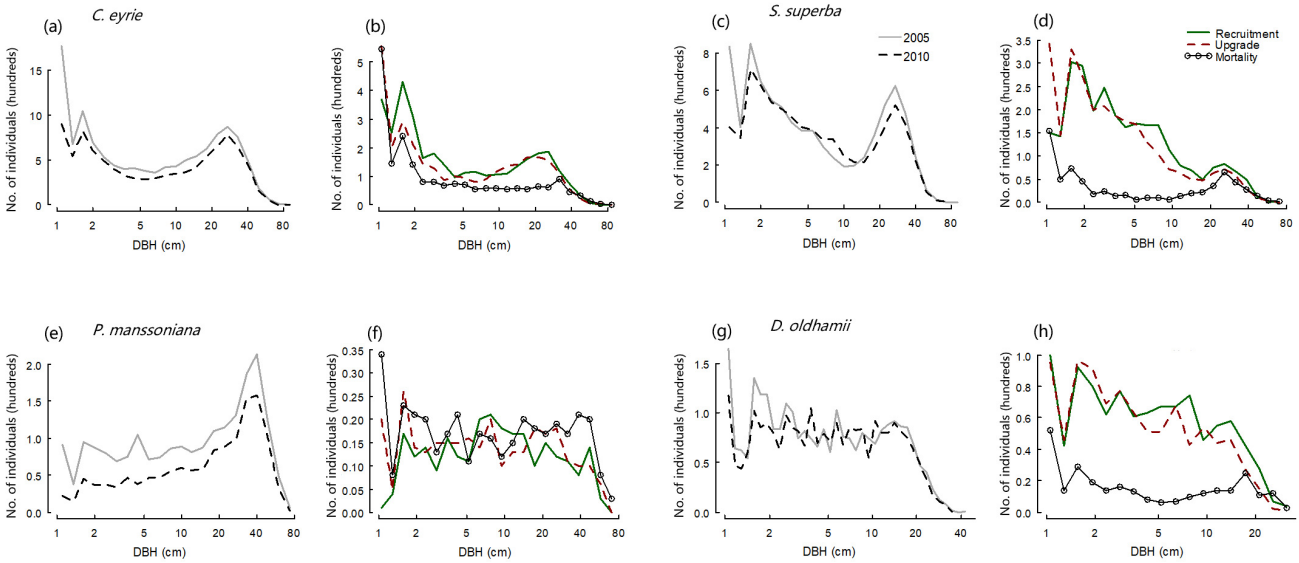


Figure 2. Diameter structure dynamics, recruitment, upgrades, and mortality of the four canopy dominant populations from 2005 to 2010. (**a**) Diameter structure dynamics of *C. eyrei*; (**b**) recruitment, upgrades, and mortality of *C. eyrei*; (**c**) diameter structure dynamics of *S. superba*; (**d**) recruitment, upgrades, and mortality of *S. superba*; (**e**) diameter structure dynamics of *P. massoniana*; (**f**) recruitment, upgrades, and mortality of *P. massoniana*; (**g**) diameter structure dynamics of *D. oldhamii*; (**h**) recruitment, upgrades, and mortality of *D. oldhamii*.

Table 2. Population dynamics of canopy layer dominant species from 2005 to 2010.

Species	Individuals in 2005	Individuals in 2010	Survivors in 2005–2010	Deaths in 2005–2010	Recruits in 2010	Mortality Rate	Recruitment Rate	Population Change Rate
Castanopsis eyrei	12,333	9651	8722	3611	929	6.93%	2.02%	−4.91%
Schima superba	8470	7663	7285	1185	378	3.01%	1.01%	−2.00%
Pinus massoniana	2060	1318	1308	752	10	9.08%	0.15%	−8.93%
Daphniphyllum oldhamii	2711	2488	2210	501	278	4.09%	2.37%	−1.72%

3.2. Differences in the Distribution of Dead Trees in Different Habitats

The four dominant populations (*C. eyrei*, *S. superba*, *P. massoniana*, and *D. oldhamii*) were mainly distributed in low valleys and low ridges (Figure 3a,e,i,m). Specifically, *S. superba* and *P. massoniana* were relatively more distributed in high-altitude areas (Figure 3e,i). From low valleys to high ridges, the density of *C. eyrei*, *S. superba*, and *P. massoniana* populations gradually increased (Figure 3b,f,j), the mortality rate of *C. eyrei* and *S. superba* populations gradually decreased (Figure 3d,h), the death number of the *C. eyrei* population gradually decreased (Figure 3c), and the death number of the *S. superba* population decreased and then increased (Figure 3g). The death number of the *P. massoniana* population was higher in the high-altitude area, and the mortality rate did not change much (Figure 3k,l). The density of the *D. oldhamii* population was higher in the low-altitude area and, from low valleys to high ridges, the death number and mortality rate were much greater at low-altitude areas than at high-altitude areas (Figure 3n,o,p).

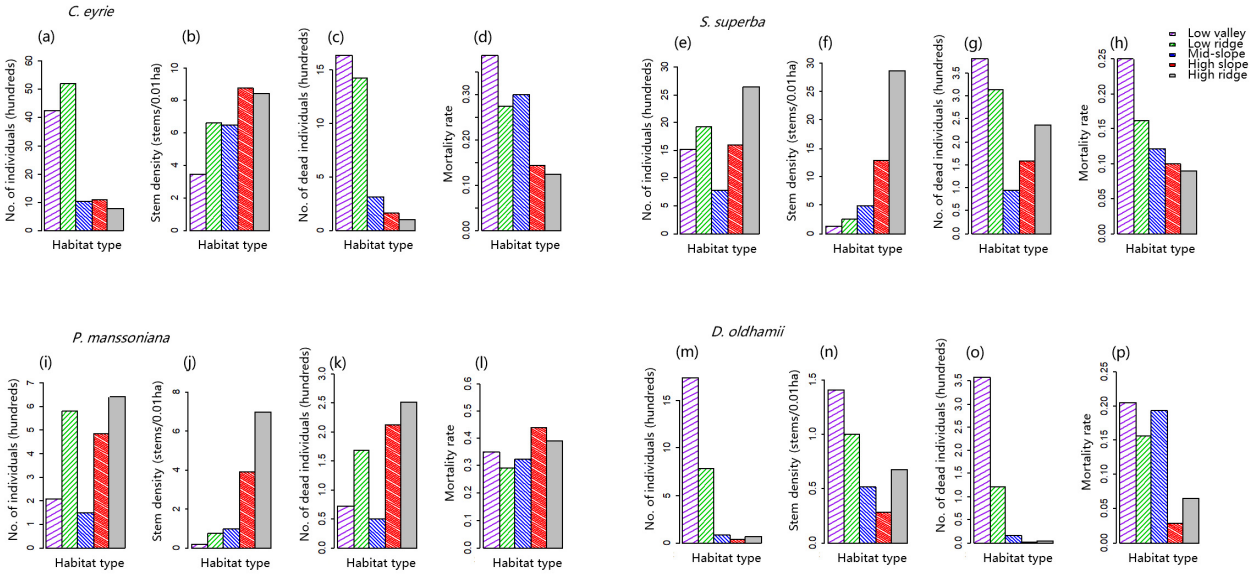


Figure 3. Distributions of dead individuals for each canopy dominant species in five habitats. (**a**–**d**) Abundance, density, deaths, and mortality rate of *C. eyrei* in five habitats; (**e**–**h**) abundance, density, deaths, and mortality rate of *S. superba* in five habitats; (**i**–**l**) abundance, density, deaths, and mortality rate of *P. massoniana* in five habitats; (**m**–**p**) abundance, density, deaths, and mortality rate of *D. oldhamii* in five habitats.

3.3. Spatial Point Patterns of Dead Trees across Life Stages

Dead *C. eyrei*, *S. superba*, and *P. massoniana* individuals, saplings, juveniles, and adults were all aggregated on the scale of 0–100 m, and the degree of aggregation from saplings to adults tended to decrease with increasing scale (Figure 4a–l). In contrast, dead *D. oldhamii* individuals, saplings, and adults were aggregated at the scale of 0–100 m, while dead juveniles were aggregated at 0–74 m but randomly distributed at 74–100 m (Figure 4m–p).

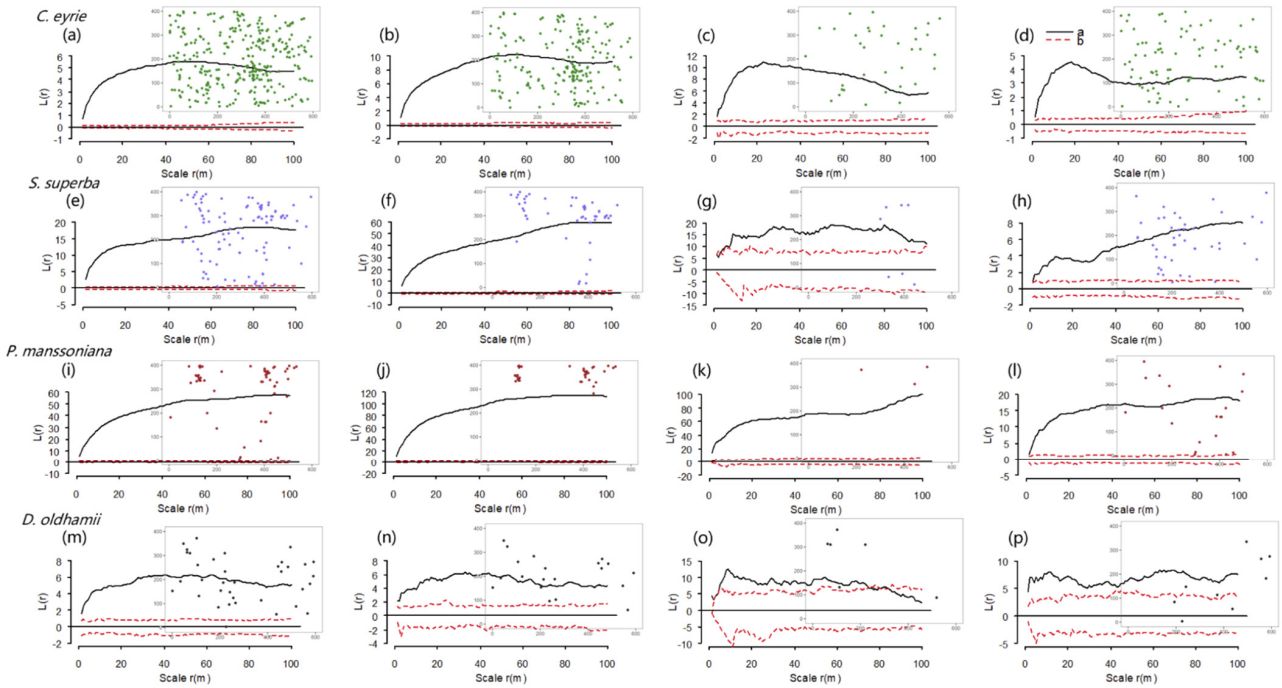


Figure 4. Spatial point patterns of dead individuals at different life stages. (**a**) All dead individuals of *C. eyrei*; (**b**) dead saplings of *C. eyrei*; (**c**) dead juveniles of *C. eyrei*; (**d**) dead adults of *C. eyrei*; (**e**) all

dead individuals of *S. superba*; (**f**) dead saplings of *S. superba*; (**g**) dead juveniles of *S. superba*; (**h**) dead adults of *S. superba*; (**i**) all dead individuals of *P. massoniana*; (**j**) dead saplings of *P. massoniana*; (**k**) dead juveniles of *P. massoniana*; (**l**) dead adults of *P. massoniana*; (**m**) all dead individuals of *D. oldhamii*; (**n**) dead saplings of *D. oldhamii*; (**o**) dead juveniles of *D. oldhamii*; (**p**) dead adults of *D. oldhamii*. Additionally, 'a'(the black line) represents the L(r) function value, 'b' (the red dashed line) represents envelopes, and 'r' represents the radius of the sampled circle from the focal tree. The top right graph shows the spatial point pattern of individuals.

4. Discussion

4.1. Effects of Extreme Winter Storms on the Population Characteristics of Canopy Dominant Species

Among the 43 dominant species in the 5-ha evergreen broad-leaved forest in Gutianshan from 2002 to 2007, 31 populations were growing populations and the other 12 populations showed small negative growth [41]. Compared to the population renewal dynamics of subtropical forests under "normal" conditions, the winter storm increased the mortality rate of canopy dominant populations and decreased the recruitment rate, resulting in the population exhibiting a negative growth trend. These results are in line with those of previous studies [19,42]. The shortfall in recruitment rate may be time-related, as the recovery period (2008–2010) was only 2 years. The large number of canopy gaps after the winter storm increased the light level within the forest understory. Competition among surviving trees decreased after the windstorm and the upgrading rate exceeded the recruitment rate, resulting in an overall increase in the plot-level DBH of the dominant populations. The lack of recruitment and the high rates of tree mortality, especially among large-diameter individuals, resulted in a decrease in the plot-level basal area of the dominant populations. In general, after the extreme winter storm, the dominant populations displayed an overall trend of increasing plot-level DBH and decreasing plot-level basal area.

Extreme winter storms cause significant damage to all species in a forest, but the extent of damage varies by species [20,43,44]. For the four canopy dominant species in the 24-ha subtropical Gutianshan forest, *P. massoniana* was most affected by the winter storm (population growth rate: −8.93%), followed by *C. eyrei* (population growth rate: −4.91%), *S. superba* (population growth rate: −2.00%), and *D. oldhamii* (population growth rate: −1.72%). Broad-leaved evergreen species and conifer species may exhibit differences in sensitivity to the winter storm due to differences in crown diameter, leaf area, tree taper (D/H), and wood properties [45,46].

We found that the diameter structure of the populations of three evergreen broad-leaved species (*C. eyrei*, *S. superba*, and *D. oldhamii*) showed bimodal and multimodal distribution. This distribution indicates that the population has developed to more advanced stages and that the whole population is relatively stable [47]. During the time of this study, there were more individuals in the large-diameter class, which inhibits the growth of the medium-diameter class trees but does not hinder the survival of the small-diameter class individuals. It is generally believed that tree mortality is related to DBH [21]. The large-diameter trees have a more extended leaf area, representing a larger snow interception area. Small-diameter individuals do not have strong trunk support and are susceptible to mechanical damage caused by the pressure of snow and nearby large tree branches. However, in the extreme winter storm in 2008, although the degree of damage to large-diameter trees increased with the increase in DBH, more serious damage, such as collapse and breakage, decreased accordingly [8]. As such, the mortality rate of the three evergreen broad-leaved species tended to decrease with increasing diameter class.

In contrast, the recruitment, upgrade, and mortality numbers for conifer species (*P. massoniana*) did not decrease significantly with increasing diameter class, and there were few recruitment individuals for the small-diameter class. This may be because the *P. massoniana* population tends to be aging and is already dominated by large-diameter individuals. As a coniferous species, *P. massoniana* possesses a trunk with low strength and low elasticity, traits which increase the degree of damage caused by snow accumulation [48]. This susceptibility results in a higher mortality rate for coniferous large-diameter individu-

als compared to evergreen broad-leaved individuals. *P. massoniana* seedlings rarely appear in the forest understory under "normal" conditions [49], and the winter storm exacerbated this by covering the ground with a thick layer of litter. This litter increased soil water conservation capacity, leading to unstable hydrothermal conditions; the decomposition process of litter is also prone to harboring microorganisms that are detrimental to the germination and growth of *P. massoniana* seeds [50].

From 2005 to 2010, the diameter structure of all canopy dominant populations remained basically stable, but the number of individuals at each diameter class generally decreased. The recruitment rate was not sufficient to offset the loss of individuals due to upgrading and mortality, as similarly found by Ge et al. [19]. Moreover, the IV of the four dominant populations did not change much, indicating that the community structure is basically stable [9] and that the 24-ha plot in Gutianshan has a certain resistance to winter storms.

4.2. Effects of the Extreme Winter Storm on Mortality for Canopy Dominant Species in Different Habitats

The damage from winter storms inflicted on tree individuals is often caused by snow accumulation [51]. Forest disasters are directly affected by topographic factors. In Gutianshan, the high altitudes are more susceptible to snow damage than the low altitudes. Similarly, there is other literature that suggests that steep slopes are more susceptible than gentle slopes [18]. Our study found that the mortality rate of *P. massoniana* was higher than the other three species in all habitats, and the dead individuals were mainly concentrated on high slopes and high ridges; the highest mortality rate was found in high slopes. This may be because *P. massoniana* is a strong, light-demanding tree species mainly distributed in high-altitude areas. Due to the slope of high slopes and high ridges, *P. massoniana* may be susceptible to the establishment of asymmetric canopy cover [52], and thus suffers from the unbalanced stress of snow which causes tree breakage or death.

In high-altitudes areas, the mortality rates of the three dominant populations (*C. eyrei*, *S. superba*, and *D. oldhamii*) were relatively low. This result is consistent with the research of Man et al. [8]. Several factors may account for these findings. It may be that the height difference between the high- and low-altitude areas of the plot is not significant enough to produce dramatic differences. Additionally, the high-altitude area has a relatively gentle slope, which may reduce the amount of uneven snow accumulation. On the other hand, more dead individuals and higher mortality rates in low-altitude habitats may be related to the relatively complete canopy structure present there. Snow damage to so dense a canopy may further damage the understory [53].

Previous research has shown that plant mortality is affected, to a certain extent, by development and distribution density. Plants with lower densities and relatively slow growth rates tend to have higher mortality [54]. Another situation is that, due to the influence of the conspecific negative density dependence (CNDD), the mortality rate is also higher when the CNDD is higher [55,56]. *C. eyrei* and *S. superba* were widely distributed throughout the different habitats and displayed relatively high mortality rates in low-altitude areas with low density. *D. oldhamii* had a higher density and mortality rate in low valleys, low ridges, and middle slopes. We tentatively conclude that the relationship between the density and mortality rate varies from species to species in different habitats, and needs to be further studied.

4.3. Effects of the Winter Storm on the Spatial Point Pattern of Dead Trees

The spatial pattern of a population refers to the relatively static distribution of individuals in a given living space, as well as the adaptations of species to environmental conditions in a certain period [57]. The spatial patterns of species are strongly scale-dependent, and patterns at different scales are closely related to specific ecological processes [58]. Zhu et al. [31] showed that the distribution pattern of each dominant species in the 24-ha plot was aggregated, which aligned with the spatial point pattern of dead individuals in

our study. All mortality patterns were aggregated, mainly due to the manner in which the winter storm led to clusters of dead individuals. Large amounts of snow falling from the canopy of adult trees can cause the death of individuals in lower layers and, since seeds usually fall near the parent tree [59], the fall of an adult tree can cause the death of a large number of individuals of the same species nearby.

Some studies have found that as the diameter class increases, the ability of individuals to acquire resources increases; under the influence of density constraints, this can mean that the degree of aggregation tends to decrease [60,61]. Generally, the distribution pattern of populations evolves from aggregated distribution to random distribution [62]. We found a decreasing trend in the aggregation of individual mortality patterns from saplings to adults, which was consistent with the distribution pattern of living saplings and adults. It is noteworthy that dead *D. oldhamii* juveniles were distributed randomly at the scale of 74–100 m, probably due in part to significant interspecific competition among the juveniles.

5. Conclusions

The changes in the population dynamics of canopy dominant species reported here indicate that extreme winter storms have variable effects on population dynamics in subtropical forests. The population dynamics of four dominant species were significantly altered following the winter storm, but the extent of the changes varied with species. More specifically, *P. massoniana* was most affected by the storm, followed by *C. eyrei*. Small-diameter individuals experienced higher mortality rates. The number of individuals, the density of the dominant population, the number of mortalities, and the mortality rate of the dominant species differed among habitats. Further studies are needed to ascertain whether there is a correlation between the density and mortality rate of a singular species that occupies different habitats and, if a correlation does exist, whether it is species-related.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/f13101634/s1, Figure S1: Map of five habitat types with multivariate regression tree analysis in a 24-ha plot. Type 1: low valley, Type 2: low ridge, Type 3: mid-slope, type 4: high slope and type 5: high ridge. More detailed information could be found in Chen et al. (2010). Figure S2: Number of dead individuals in each life stage (dead sapling; dead juvenile; dead adult) of four canopy dominant species (*Castanopsis eyrei*, *Schima superba*, *Pinus massoniana*, and *Daphniphyllum oldhamii*).

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